A COMPARISON OF THREE NATURAL SUCCESSION CHRONOSEQUENCE CASE STUDIES FROM THE SOUTH ISLAND, NEW ZEALAND TO SELECT PREDICTABLE INDICES FOR EVALUATING RESTORATION SUCCESS

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To 'La Pacha Mama'

long may she live and give life

ABSTRACT

Evaluating the success of ecological restoration interventions in establishing self-sustaining development toward distant goals within project timescales is problematic. Trajectory analysis is a promising evaluation strategy to this end yet it has received little research attention and is uncommonly used. This thesis aims to identify indices predictable enough to be suitable for trajectory analysis, focusing plant assemblage structure. The primary objectives were to: a) accurately infer plant assemblage development gradients of primary successions in three different ecosystems of the South Island, New Zealand by means of sampling well aged chronosequences, and b) establish which indices had sufficiently strong and consistent response trajectories to all three inferred vegetation development gradients to be considered predictable. The vascular plant assemblages of at least five development stages in each of the three sites were sampled intensively using multiple fixed area plots. Ordination and stepwise regression established that age was highly correlated with the main floristic gradient and environmental variables were unimportant in explaining floristic variation. Data for index calculation consisted of plant species cover abundance and leaf area estimates as well as soil chemical properties. Development stage age estimates enabled index response trajectories to be constructed from stage mean values. Regression models were fitted to observed index trajectories for each site to test response strength and predictability. Comparisons of regression statistics and trajectories among the three sites for each index showed that the majority of indices had predictable responses to all sites; these were: soil pH and organic carbon, importance score, Simpson's species diversity, distance from the lognormal model of species relative abundance distribution, growth form diversity, taxonomic distinctness and DCA axis one. Together, these indices are suggested to be able to evaluate if development trajectories indicate progress towards three restoration goals via intermediate objectives. These goals are: 1) a persistent plant assemblage, 2) a plant assemblage with specific structural attributes and 3) a well functioning ecosystem. For trajectory analysis to effectively evaluate restoration success with these goals it is recommended that recovery gradients are long, monitoring periods are at least three decades and multiple indices are used that convey complementary information.

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ABBREVIATIONS OF COMMONLY USED TERMS.

DCA	Detrended Correspondence Analysis
DCCA	Detrended Canonical Correspondence Analysis
PCA	Principal Components Analysis
ANOSIM	ANalysis Of SIMilarities
RAD	Relative species Abundance Distribution
DS	Development Stage
RECCE	REConnaissanCE vegetation sampling method
DoC	New Zealand Department of Conservation
DBH	Diameter at Breast Height
EDA	Exploratory Data Analysis
SSD	Soft Sediment Depth
FALL	Fixed Area Largest Lichen
VIF	Variance Inflation Factor
df	degrees of freedom

1 GENERAL INTRODUCTION

1.1 OVERVIEW

This chapter provides a current perspective on the science and practice of ecological restoration with an emphasis on evaluation. It begins by defining what restoration is in terms of the types of ecosystem recovery it has been able to achieve. The main body of the chapter highlights how the conceptual framework of restoration ecology provides both challenges and guidance for effective evaluation as well as identifying research priorities. A brief review of current evaluation methods then illustrates how restoration practice lags behind theory. Finally, the scope, objectives and structure of the thesis is outlined.

1.2 THE HISTORY OF ECOLOGICAL RESTORATION

1.2.1 WHAT IS ECOLOGICAL RESTORATION?

In this thesis, the definition of ecological restoration follows that in a recent working document published by the Society for Restoration Ecology International; "the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed" (SER Science and Policy Working Group 2004, p 3). Ecological restoration interventions are normally only justified if a degradation threshold has been crossed that prevents natural recovery, or, if natural recovery is perceived to be too slow. Ecological restoration techniques usually aim to remove degrading forces and to speed or steer succession so that a system with desired attributes develops. The theoretical end point of restoration is a vision that is agreed by all stakeholders in the project and defined by the desired states of various system attributes. These states are commonly referred to as the 'goals'. Irrespective of the system states that the goals may describe, a common interim objective is the establishment of sufficient natural processes to enable the system dynamics to be maintained without further intervention, whether they are in relative equilibrium or are still moving along a development gradient. Further intervention beyond the restoration end-point would be better described as ecosystem management.

Restoration projects vary in many respects including spatial extent, management intensity and precision. Thus, when considered together projects occur along a continuum encompassing for example: localised restoration from bare substrate, extensive restoration

of productive lands such that their production is ecologically sustainable, managing landscapes for connectivity, and enhancing specific values of conservation lands. A diverse terminology has evolved which attempts to compartmentalise this continuum of ecological restoration endeavours. For example, terms used in the past include: creation, reclamation, rehabilitation, reallocation, replacement, reconstruction and enhancement (e.g. Westman 1991; Bradshaw 1996; Dobson et al. 1997; Whisenant 1999; Ehrenfeld 2000) as well as restoration *sensu stricto* and *sensu lato* (Aronson et al. 1993). However, these terms have often led to confusion instead of clarity (Hobbs & Norton 1996). An important result of this terminological confusion has been to shift the focus away from discussing the goals, which are in fact the most useful means of defining restoration (Hobbs & Harris 2001).

1.2.2 WHAT IS RESTORATION ECOLOGY?

Restoration ecology is the synthesis and application of ecological theory to the specific problems involved in assisting the recovery of ecosystems. As such it is the 'acid test' of ecology *sensu* Bradshaw (1987) and is a relatively novel field of ecology.

1.2.3 A SHORT HISTORY OF ECOLOGICAL RESTORATION AND RESTORATION ECOLOGY

Recorded ecological restoration attempts date back to the early 20th century, beginning on ex-mine sites (Choi 2004). As a professional field it is probably less than twenty years old (Halle & Fattorini 2004). Recently ecological restoration has been increasingly viewed as an essential tool for achieving sustainable development and biodiversity conservation objectives alike (Higgs 1994; Naveh 1994; Daily 1995; Dobson et al. 1997; Urbanska et al. 1997; Rana 1998; Whisenant 1999; Norton 2000; Urbanska 2000; Hobbs & Harris 2001) owing to many encouraging successes. Indeed, a recent review of all papers published in the Journal of Applied Ecology over the last 40 years (Ormerod 2003) showed that restoration efforts had more success than non intervention at achieving conservation gains at the species, ecosystem and landscape level.

Ecological restoration in New Zealand has been formally practiced for c. 40 years (Atkinson 1994) with an explosion of projects during the last 15 years. Projects in New Zealand vary widely in their stakeholder profile, scale and goals; ranging from enhancing biodiversity values of the conservation estate (Towns et al. 1990; Towns & Ballantine 1993; Saunders & New Zealand Dept. of Conservation 2000; Saunders & Norton 2001)

and of other public and private lands (New Zealand Ecological Restoration Network 2005) to mine site rehabilitation (e.g. Norton 1991).

A major focus for restoration ecology today is the development of a robust yet general conceptual framework such that practicioners and scientists can engage in a discussion of problems and solutions independent of system or location (Clewell & Rieger 1997; Hobbs & Harris 2001; Halle & Fattorini 2004). There have been several key contributions to the development of such a framework (e.g. Aronson et al. 1993; Hobbs & Norton 1996; Allen et al. 1997; Urbanska et al. 1997; Whisenant 1999; Hobbs & Norton 2004). However, the framework is still very much under development (Halle & Fattorini 2004). Indeed, the ideas presented and questions posed by Hobbs & Norton (1996) almost ten years ago are still relevant today. Nonetheless, application of the conceptual models as they stand to a standard project management approach would create benefits. These benefits would result from the development of restoration projects based on ecological principles, thus enabling: the formulation of realistic goals, more effective evaluation of projects and the synergy of currently dispersed practical knowledge. Furthermore, the increased levels of feedback that a more standard approach would allow should act to verify and modify the ecological models that comprise the conceptual framework itself.

The level of biological organisation at which most restoration projects to date have operated is the community (Lockwood & Pimm 2001). Many restoration projects operate at the population level but very few operate at the ecosystem level (Cairns 1995), despite repeated calls for restoration to be integrated in the context of the wider landscape (Naveh 1994; Aronson & Le Floc'h 1996; Whisenant 1999; Patil et al. 2001). The focus on the community level possibly reflects the fact that community ecology forms the basis of the restoration ecology conceptual framework. Furthermore, the focus on plant communities may be because those models most heavily drawn upon by community ecology (succession and assembly) have their primary empirical basis in plant communities (Young et al. 2001). A powerful aspect of restoration ecology is that it has stimulated a synthesis of succession and assembly theories (e.g. Hobbs & Norton 1996; 2004) which historically have largely been considered separately, despite them being complementary approaches to understanding community development.

1.3 ACHIEVING BETTER EVALUATION OF SUCCESS: A KEY CHALLENGE FACING ECOLOGICAL RESTORATION

This thesis focuses on one challenge facing ecological restoration that in my view, and that of others (e.g. Westman 1991; Hobbs & Norton 1996; Hobbs & Harris 2001) is key to the advancement of the field: developing reliable means to evaluate the success of restoration projects. Evaluation of success is critical for a multitude of reasons. In particular it forces the project goals to be defined at the start of the project and encourages ongoing monitoring such that management techniques can be adapted if necessary. In addition, it enables exit strategies to be followed that would leave all stakeholders more satisfied; increasing the likelihood of future monetary, logistic and political support not only for those involved in the project but also for future restoration projects in general.

1.3.1 BARRIERS TO THE EVALUATION OF RESTORATION SUCCESS

Evaluation can be approached from cultural, economic, abiotic and biotic perspectives, however, this thesis is limited to considering the biotic perspective. From a biotic perspective, there are a wide range of attributes required to fully describe the state of any ecosystem. A recurring theme in restoration ecology is what attributes to base goals upon and which are the priority. The most frequently suggested and used attributes are community structure, function and composition (Westman 1991; Hobbs & Norton 1996; Ehrenfeld & Toth 1997; Palmer et al. 1997). Less promoted ideas include resilience, heterogeneity, keystone species and organisation (i.e. connectedness among individuals) (Aronson et al. 1993; Hobbs & Norton 1996; Higgs 1997; Rapport 1998).

Evaluation of restoration success for a community relies upon two basic preconditions being met. Firstly that the goals defined are achievable. Secondly that the goals can be measured by simple parameters that respond to recovery in predictable ways such that progress towards them can be assessed. Both of these preconditions are problematic. The following two sections discuss the barriers to meeting these preconditions with the aim of making it clear why evaluation attempts in the past have been confounded and where some solutions lie.

1.3.1.1 What is a realistically achievable goal? Lessons from ecosystem development theory.

Common practice in restoration has been to define goals by identifying an ecosystem that exists within the zone of similar biotic and abiotic conditions to the reference site and is considered to be in a relatively undisturbed state. Such a system is termed the 'reference system'; the state of which is assumed to represent a desirable goal in terms of the attribute of interest. However, this practice is problematic. Firstly, reference systems are often scarce and degraded (Simberloff 1990; Aronson et al. 1995) and their states may not correspond with environmental conditions at the time of measurement due to inertia (White & Walker 1997). In addition, it is difficult to decide how much spatial variability to sample. If sampling is from a limited spatial extent only then goals become very specific (Cairns 1989). Specificity is the most intractable problem with goals derived from reference systems because modern theories of community dynamics indicate that specific goals are unattainable (Palmer et al. 1997; Ehrenfeld 2000; Hobbs & Harris 2001). Moreover, in the context of environmental change, such static goals are futile (Hobbs & Norton 1996; Choi 2004)

The central tenet of modern community ecology is the dynamic equilibrium paradigm which views ecosystems as spatially and temporally variable because of the effects of stochastic disturbances (Pickett & White 1985). As a consequence of this paradigm, traditional views of succession leading deterministically to a stable 'climax' with a predetermined community structure and composition are no longer accepted (Pahl-Wostl 1995). Furthermore, assembly theory suggests that the dynamics of any given succession depends on contingent circumstances (Noble & Slatyer 1980) including disturbance history and the sequence of species invasions ('priority' effects). Thus, identical sets of available species have the potential to assemble into alternative states under different circumstances (Buss & Jackson 1979; Connell 1980; Drake 1990). Nonetheless, despite the stochastic and probabilistic nature of assembly processes, empirical evidence shows that community development is often predictable, at least for structural parameters to the extent of normal values found within a region (Palmer et al. 1997; Drake et al. 2001a). Assembly theory includes two main reasons for predictability at the regional level. Firstly, constancy in environmental conditions creates a repetition of available species pools and safe sites provision (Hobbs & Norton 1996). Secondly, with a certain resource availability the outcomes of competitive interactions between particular colonising species appear to be set (Austin & Smith 1989; Drake 1991). In addition, certain

assembly rules exist that reproduce structural patterns in communities independent of the species involved (Diamond 1975; Wilson et al. 1996; Samuels & Drake 1997; Wilson 2001b). However, specific compositional predictability often remains elusive because of priority effects and the number of species interactions within a complex ecosystem being too large to model even if all competitive interactions are known (Walker & del Moral 2003).

The model of community development favoured by most restoration ecologists seems to be the Alternative Stable State (ASS) model. This model forms a middle ground between wholly deterministic and stochastic viewpoints. The ASS model asserts that community development is predictable to the extent that the potential states fall within 'a domain of attraction' (Pimm 1984), which is analogous to 'basins of attraction' in complexity theory (Kauffman 1993). Therefore, the modern conceptual framework of restoration ecology promotes that goals should be derived from a range of reference states representing the likely range of dynamic equilibrium states attainable (Hobbs & Norton 2004), rather than from a single state.

1.3.1.2 Lack of easily measurable and predictable parameters

The second major barrier to evaluating success is unpredictable behaviour of the parameters used to quantify goals. This thwarts evaluation as in most cases evaluation attempts to assess whether the extent of recovery attained provides sufficient evidence that the system is likely to undergo continued change in the direction of the goals. States along a suitable development trajectory have been termed objectives or 'success criteria' (Hobbs & Norton 1996). Such objectives are used either if the final evaluation has to be made before the system has had time to reach goals, or, if monitoring is employed to support an adaptive management approach. If the system has reached a dynamic equilibrium within the evaluation period, then evaluation parameters do not need to be predictable. This scenario is ideal and by no means usual so is not dealt with here.

There are two major reasons for unpredictability of parameters; unknown future development trajectories and irregular response of parameters to the natural successional processes occurring in any development gradient.

Unfortunately, predicting the future trajectory of system development is a distant possibility. Trajectory dynamics have been incorporated within the restoration ecology conceptual framework using the state and transition model (Hobbs & Norton 1996, 2004). This model views change as a series of transitions between meta-stable states owing to

non-linear responses to environmental factors. Multiple meta-stable system states can be envisaged as troughs along a single successional trajectory (Young et al. 2001; Hobbs & Norton 2004), as well as nodes of a trajectory network or bifurcation points of divergent trajectories leading to alternative stable states (Walker & del Moral 2003). Transitions between states have thresholds associated with them which can act as a barrier to recovery if they are difficult to cross (Hobbs & Norton 1996). However, transitions can also be precipitated by random events. In addition, the whole process is seen as influenced by a set of filters that act to limit the availability of species for colonisation. Filters can be abiotic (climate and disturbance regime) or biotic (species interactions) (Whisenant 1999) and represent gradients of resistance to restoration (Hobbs & Norton 2004). The state and transition model does not offer any specific answers to the outcomes of recovery trajectories but it focuses the restorationist on understanding the factors in each system that require manipulation in order to control trajectories, i.e. variables driving state transitions and resistance filters. Successional models describe the mechanisms and processes by which ecosystems develop (Egler 1954; Connell & Slayter 1977; Grime 1979; Noble & Slatyer 1980; Pickett et al. 1987b, a; Walker & Chapin 1987), yet they too fail to predict the occurrence or outcome of trajectory divergence or bifurcations, even when incorporated into modern computer simulations (Walker & del Moral 2003).

An advance that is possible in the medium term is to identify parameters that respond predictably to the process of succession. There have been calls for research to test parameter response among different development gradients to this end (Hobbs & Norton 1996), however very few comparative studies of different successional series have been done (Walker & del Moral 2003). Therefore, parameters that are adequate for measuring restoration success in a variety of ecosystems are yet to be established. Whilst the availability of such parameters will not solve the issue of unpredictable development trajectories discussed previously, their use would still enable the confidence of evaluation judgements to be improved.

1.3.2 CURRENT RESTORATION EVALUATION PRACTICE

This section provides a summary of the strategies used to evaluate success and which parameters are most commonly measured. To form the basis of this summary, I conducted a survey of 35 peer reviewed journal articles published between 1990 and 2004 that detailed restoration evaluation techniques (citations are listed in Appendix one).

1.3.2.1 Strategies for evaluating success currently employed

Strategies for evaluating restoration success can be categorised into three types: direct attribute comparison, attribute analysis and trajectory analysis. The strategy chosen depends on the resources and type of reference information available as well as the proximity of goals. However, a key issue affecting the effectiveness of all strategies is the short time period that normally elapses before a judgement of success is made. One review of 87 projects (Lockwood & Pimm 2001) reported that the mean time after project initiation at which evaluation attempts were made was only 6.3 years.

The most common of these appears to be direct comparison. Direct comparison involves comparison of parameter values between the reference and restoration site (e.g. Findlay et al. 2002; McCoy & Mushinsky 2002; Longcore 2003). Attribute analysis involves the use of mostly semi-quantitative data to make an ecological assessment about the status of key attributes (e.g. Duel et al. 1995; Keddy & Drummond 1996). For example, a key attribute may be that the physical environment is capable of sustaining reproducing populations of the species necessary for its continued development or stability.

Trajectory analysis is most suitable if the ecosystem being restored is not likely to come within close proximity of the goals within the project life-span. However, despite its promise, trajectory analysis is uncommon and in need of development (SER Science and Policy Working Group 2004). Hence, this thesis seeks to conduct research that can be applied to the development of trajectory analysis methods. Trajectory analysis involves periodical collection of data on key attributes from the restoration site, which are then plotted to provide a representation of the development trajectory. The trajectory is assessed to establish whether or not the trend is leading towards a suitable condition.

1.3.2.2 Common attributes and parameters used to evaluate success

Among the 35 articles reviewed (each of which pertained to a different restoration project), a total of 98 parameters were measured from 20 types of parameter. The 20 types were all related to one of three ecosystem components: the plant community, the animal community and soil properties or biota. The most common component measured was plant communities and within this, the most frequently used parameters were taxonomic richness and multivariate composition. Other common parameters were indicator species, plant cover or density, soil chemistry and vegetation physiognomy. Therefore, the parameters mostly measured structural and compositional attributes. Direct measures of function were uncommon although inference about function and process from indicator values and

pattern was relatively common (e.g. Reay & Norton 1999; Wilkins et al. 2003). Table 1.1 below lists all 20 parameter types and their use frequencies. The citations for the 35 articles are listed in Appendix one.

Evaluation parameter	Frequency of use	Ecosystem component measured	Frequency of use
Soil chemical properties	9		
Soil structure	3	Soil	20
Microbial processes	5		
Microbial biomass	3		
Plant total biomass	1		
Similarity indices plant assemblage	5		
Plant indicator taxa presence/density	3		
Plant species diversity (relative abundance measures)	2		
Plant species, or higher taxonomic level, richness	12		
Growth form (dominant form /richness of forms)	3	Plant	51
Multivariate plant assemblage composition	9		
Physiognomy	7		
Plant spatial distribution pattern	1		
Plant cover / density (not taxonomically split)	6		
Plant processes (recruitment/dispersal)	2		
Similarity indices of animal assemblages	4		
Animal species diversity (relative abundance measures)	2		
Animal species, or higher taxonomic level, richness	9	Animal	27
Multivariate animal assemblage composition	7		
Animal indicator taxa presence/population data	5		

Table 1.1 A summary of the indicators used to evaluate restoration success that were reported in 35 peer reviewed English language journal papers published from 1990 to 2004. Each paper refers to a different ecological restoration project, all of which were in terrestrial or freshwater systems. A total of 98 indicators were used which relates to an average of c. three indicators per study (i.e. per evaluation attempt). Indicators are grouped into 20 types for ease of comparison.

1.4 THESIS SCOPE

1.4.1 PROBLEM STATEMENT – AN UNDEVELOPED TRAJECTORY ANALYSIS 'TOOL-BOX'

The conceptual framework of restoration ecology is sufficiently developed for appropriate goals to be set and evaluation strategies to be applied. However, ecological

restoration projects commonly fail to evaluate recovery on a scientific basis, leading to poorer management and a loss of opportunity to improve knowledge of system dynamics and intervention techniques.

Trajectory analysis is perhaps the most promising evaluation strategy for restoration projects where success must be judged before goals are reached. A major barrier to effective evaluation using trajectory analysis is the absence of a 'tool-box' of predictable indices that measure community structure and function. Such indices need to be not only relevant to common goals but also have responses to succession that are known to be consistent in a variety of ecosystems. Furthermore, the use of such a tool-box to predict successful accomplishment of goals from the achievement of intermediate objectives is hindered by the trajectory analysis evaluation strategy being underdeveloped.

To address the problem, the following aims, objectives, and questions were elaborated which together define the thesis scope. To clarify the scope further, the type of restoration endeavours which the thesis conclusions apply to are also described.

1.4.2 THESIS AIM AND OBJECTIVES

1.4.2.1 Thesis aim

To facilitate the evaluation of restoration success by trajectory analysis through testing predictability of indices' response to vegetation development gradients, focusing on indices of plant assemblage structure.

1.4.2.2 Thesis objectives

1. Sample three entire primary succession vegetation development gradients by means of chronosequence development stages.
    a. Ensure each succession is in a different ecosystem with different natural disturbance regimes so as to sample a variety of structural dynamics that together provide a breadth of analogues for vegetation recovery resulting from restoration interventions.
    b. Bias sampling toward the earlier part of the vegetation development gradients because change tends to be fastest during this part.
2. Devise sampling methodologies that:
    a. Measure the majority of the natural variability in species diversity occurring within each development stage.

b. Reduce as far as is possible the variation of any environmental factors that may confound the vegetation development inferred by chronosequence.

3. Test the response of a suite of commonly used and novel indices to the three vegetation development gradients.
4. Compare response of indices to assess:
    a. Index variability among replicate samples of the same development stage.
    b. Differences among indices response trajectories to the same vegetation development gradient.
    c. Trajectory predictability for each index among different vegetation development gradients.
5. Recommend indices to evaluate restoration success using the trajectory analysis strategy.

1.4.2.3 Thesis questions investigated

I. How do floristics vary with age and does the main floristic gradient correlate more closely with age than any other environmental variable?

II. Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?

III. Which indices have strong and consistent responses to all three case study vegetation development gradients; i.e. which of the tested indices have predictable enough responses to be suitable for the evaluation of restoration success via trajectory analysis?

IV. What restoration objectives and goals are the indices suitable for trajectory analysis able to evaluate?

1.4.2.4 The types of restoration endeavour to which this thesis applies

Owing to the case studies characterising entire primary succession development gradients, this thesis is most applicable to restoration endeavours that attempt to "create" ecosystems (i.e. those which start from bare inorganic substrate or poor soils with no viable propagules). Therefore, in order to be manageable and maintain focus, the results of this thesis are only interpreted in terms of this type of restoration and do not consider restorations that attempt to change existing systems.

Restorations involving creation of new ecosystems encompass two of five possible kinds of restoration identified by the Society for Ecological Restoration International (Clewell et al. 2000); modified descriptions of these follow:

1. Creation of a new ecosystem of the same kind to replace one that has been entirely removed.

The term creation signifies that the restored ecosystem is entirely reconstructed on a site denuded of its vegetation. The specification that the new ecosystem would be of the same kind implies the availability of good reference information. A New Zealand example of this would be a mine site in an area of northern Westland, South Island which would probably be surrounded by native vegetation in a range of successional states associated with the natural disturbance regime.

2. Creation of a replacement ecosystem because insufficient reference information exists to serve as a model for restoration.

This option is relevant for areas of the world where intensive historic land use has removed all or almost all remnants of original ecosystems. However, it is always possible to piece together some information to guide restoration efforts, albeit piecemeal or pertaining to a quite distant remnant. A New Zealand example of this would be the lowland forest of the Canterbury Plains, South Island of which only one small and degraded remnant (Riccarton Bush) remains.

1.5 THESIS STRUCTURE

The structure of the thesis follows the order of the five thesis objectives outlined previously, and tests the four thesis questions in sequence. It has six further chapters:

Chapter two; the general methods chapter, covers the methods to test the first two thesis questions in sequence.

Chapters three, four and five; each take a case study chronosequence with which to test thesis questions I & II in order. The first case study is of a forest system that develops after landslide disturbance. The second case study is of a herbaceous grassland system that develops after flooding disturbance. The third case study is a forest system that develops after a mixture of glacial and pro-glacial river disturbance. Case studies are dealt with in chronological order of the field work.

Chapter six; compares the index behaviour among sites, covering thesis question III to identify which indices have predictable enough responses for use in the trajectory analysis restoration evaluation strategy.

Chapter seven; is the final discussion chapter that draws upon the results from investigating the former three thesis questions. It considers the fourth and final thesis question relating to which restoration objectives and goals the predictable sub-set of tested indices are suitable to evaluate using trajectory analysis.

1.6 DEFINITION OF TERMS

For clarity and consistency, the specific meanings of important terms in this thesis are defined here.

1.6.1 GENERAL TERMS

- **Surface** - A zone upon which vegetation development takes place that is assumed to be of equal age and physical nature throughout its extent.
- **Age** - Time elapsed since first colonisation took place on a surface.
- **Development stage** - A state along a vegetation development gradient sampled by means of a surface within a chronosequence.
- **Ecological legacy** - Any influence upon the present biota of relicts from the pre-disturbance ecosystem such as living organisms, organic matter or non-geological physical structures (Swanson & Franklin 1992).

1.6.2 TERMS RELATING TO PLANT ASSEMBLAGE OR ECOSYSTEM ATTRIBUTES

- **Composition** - The species or functional groups present within an assemblage.
- **Structure** - Any feature of the ecosystem components (i.e. species) themselves that does not deal with the identity of the species.
- **Function** - The rate or level of an ecosystem process.
- **Process** – Material or energy flow through or within an ecosystem as well as the formation of biological structure and physical elements.

1.6.3 TERMS USED TO DESCRIBE THE BEHAVIOUR OF INDICES TO THE VEGETATION DEVELOPMENT GRADIENTS:

- **Response** - The reaction of the index to the vegetation development gradient.
- **Sensitive** - An index with a large response relative to the unit of measurement.
- **Trend** - A net change, in either a positive or negative direction, over the entire length of the vegetation development gradient.
- **Trajectory** - The path of index response over time.
- **Irregularity** – an alteration of direction within the path of a trajectory.
- **Consistent** - A type of trajectory where index change is unidirectional over the entire vegetation development gradient, except for one irregularity at most.
- **Inconsistent** - A trajectory where the direction of the index response changes along the vegetation development gradient. Note a change in slope associated with a levelling or steepening pattern does not constitute a change in direction.
- **Smooth** - A term referring to a near perfect linear trajectory or a curved trajectory in which the curved part has a gradually changing slope.
- **Predictable** - An index is predictable when it has a consistent trajectory with a significant trend. Predictability implies that the index can be expected to continue changing in the same direction in response to further vegetation development.

2 GENERAL METHODS

In this chapter, the elements of the field and analysis methods which are common to Chapters three, four & five are detailed. Whenever common methods described in the present chapter are referred to in any of the three following chapters, the phrase 'standard thesis methods' will be used. The methods sections of chapters three, four & five only detail variations from these standard methods specific to each site.

2.1 FIELD METHODS

2.1.1 SAMPLING DESIGN

2.1.1.1 General strategy

The general strategy for the sampling design was to satisfy a series of preconditions relating to the quality of data required to test the first three thesis questions presented in section 1.4.

Firstly, in order for successional trajectories to be accurately inferred, it was imperative that each study site represented a good chronosequence. The term chronosequence dates back to Jenny (1941), however, the method has been used since the inception of the ecology discipline in a wide variety of systems (Pickett 1989). In terms of vegetation dynamics, a chronosequence *sensu stricto* is a 'space-for-time substitution': a spatial representation of a temporal sequence of vegetation change split into development stages among which environmental factors other than time are assumed to be unimportant (Pickett 1989).

The main shortcomings of the chronosequence approach to studying succession are detailed in a thorough and often cited review by Pickett (1989). To summarise Pickett's main arguments:

- Success is dependent on good dating of development stages.
- Time is a surrogate variable for a series of past operational environments whose particulars and effects on assemblages (i.e. contingency *sensu* Noble & Slayter (1980)) cannot be known.
- The sparsity of the record through time as inferred by development stages prevents the evaluation of rates of change and the degree of trajectory linearity.

- The method effectively averages heterogeneity of vegetation dynamics on the temporal and spatial scales, obscuring mechanisms of succession (e.g. dispersal and competitive interactions).

The alternative to the chronosequence approach is direct observation through long-term studies. This does not allow the analysis of primary successions owing to the great time span of this process for most assemblages. However, it can provide some verification of chronosequence inferences (Matthews 1999). The longest potential period for observation of primary succession in the literature is at Glacier Bay, Alaska where permanent quadrats were initiated by Cooper in 1916 (Cooper 1923). However, these quadrats have only been revisited sporadically, rendering space for time substitution an untested assumption for primary succession in Glacier Bay (Walker 1995) and beyond (Pickett 1989).

In practice, chronosequences are often applied to experimental circumstances in which the assumption of equal environmental histories is violated (Walker & del Moral 2003). Nonetheless, the consensus view appears to be that there have been many successful applications of chronosequences, for the study of general structural trends of plant succession in particular (Pickett 1989; Matthews 1992) that demonstrate repeatability of regional or coarse-scale patterns of vegetation development. High levels of success with plant succession possibly reflect the strong vegetation dynamics and long gradient lengths that often occur (Walker & del Moral 2003).

Finding a good chronosequence and sampling it well is difficult. Nonetheless, in this study, every effort was made to eliminate environmental variables pertaining to initial conditions that might confound a chronosequence *sensu stricto* by applying plot location criteria to all sample sites. Variables that did prevail despite plot location criteria were measured to enable an estimation of their contribution to floristic variation, thus testing their importance. Nonetheless, it is acknowledged that a small proportion of the floristic variation within each development stage is likely to be a result of unknown/unmeasured environmental variables that may have been active during any time of their development history. The introduction of each study site descriptive chapter contains a summary of the particular variables other than time that I perceived to possibly affect the chronosequence quality at each site. However, one variable common to all sites is an unquantifiable change in species pools over the duration of history that each chronosequence spans.

Further to the sampling of an adequate chronosequence, the key aims of the sampling design were to ensure that samples (fixed dimension square plots) were: 1) large

enough to reflect the scale of individual plants and of plant species diversity, 2) spatially independent of each other, and, 3) representative of the natural floristic heterogeneity present within each development stage. Furthermore, for comparisons of species diversity statistics among the distinct plant assemblages that occurred within the development stages of each site to be robust (Magurran 2003), the design attempted to keep sampling effort sufficient (reasonably exhaustive)[1] and even among the development stages. Finally, it was imperative to sample enough replicates[2] to provide the 'power' for floristic differences among stages to be statistically significant despite the level of natural variation present within each stage. The approaches taken to these sampling design issues are discussed in the following three sections.

2.1.1.2 Plot size

The best approach for species diversity studies where different assemblages are to be compared is to standardise plot size unless there are firm grounds for deciding otherwise (Pielou 1975). In this case, the precise size to use was a trade off between time available and meeting the fundamental requirement of this study that the species richness and relative abundance distribution (i.e. the species diversity) of all the development stages was encapsulated. In practice, methodologies of past studies were used as a guidance to decide appropriate plot size.

To test if plot size had been suitable to sample species richness, smoothed species accumulation curves were examined for any inflexion. The accumulation curves were constructed from field data using GenStat (GenStat Committee 2003); smoothing involved

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[1] Reasonably exhaustive sampling is defined by visually assessing the species accumulation curve as having passed through one or more inflexions so as to have flattened off considerably but not necessarily enough to have approached the asymptote (Magurran 2003).

[2] For the two forest sites and also to a lesser extent in the grassland site, replicates are strictly speaking sub-samples and as such are pseudoreplicates. However, study sites within the South Island that would have provided 'true' replication of whole chronosequences within minimal environmental distance of one another do not exist.

an automated procedure whereby the average of 50 repetitions of accumulating samples was taken. Any early inflexion was interpreted as evidence of sufficient plot size because the majority of species must therefore have been common to all samples. Furthermore, an early inflexion means that species richness was being sampled to such a level that the novel species of the latter few replicate samples are comprised of rarer species only.

The constraint of even plot size presents a problem for the sampling of true relative abundance distributions across the considerable gradient of individual plant size with increasing vegetation development. For example, plot size had to be large enough to sample individuals of the large tree species in the oldest development stages of the forest sites without introducing either an artificial skew into the relative abundance distribution of the species assemblage, or, a spuriously high floristic variation between plots. Plot sizes for sampling each individual vegetation development gradient are discussed in Chapters three, four & five.

2.1.1.3 Sampling effort

With plot size confirmed, the decision remained of how many replicate plots to sample to obtain an adequate sampling effort. Sufficient replicate numbers were estimated by examination of the species accumulation curves constructed with partial data sets (of four plots) attained part way through the field work at each site. By estimating the minimum number of replicates required before the field season was finished, field time could be managed in order to optimise the trade off between the number of replicates per stage versus development stages sampled. Species accumulation curves were constructed with the full data sets to check that the replicate numbers sampled were in fact sufficient.

Species richness estimates are notoriously sensitive to sampling effort (Magurran 2003). As such species richness is considered to be the best test statistic with which to evaluate the effectiveness of any sampling design in producing adequate sampling effort (Lande et al. 2000). Therefore, to ensure that sampling effort was equally sufficient among development stages, the proportional difference between species area accumulation data ('S_{obs}') and estimated values of 'S_{max}' for each stage was compared among stages. S_{max}, (*sensu* Colwell & Coddington 1994; Magurran 2003) is the theoretical maximum species richness in the entire species assemblage that would be recorded for each development stage if their total extents were sampled. S_{max} was calculated with the non parametric estimator 'Jacknife 1' (Burnham & Overton 1978; Heltshe & Forrester 1983), using

complete data sets for each development stage. The 'EstimateS' computer programme (Colwell 1997) was used to do the computations with default options selected.

The choice of Jacknife 1 is based upon comparisons of the performance of multiple estimators with the data from this study combined with the recommendations of Magurran (2003)[3], who reviews the literature on the comparative performance of species richness estimators. Jacknife 1 results compared favourably to results for other estimators that were automatically calculated by EstimateS (e.g. Jacknife 2, Chao 2, Michaelis-menten & Bootstrap) in terms of the stability of richness estimates with increasing sample size and their standard deviation. In addition, the Jacknife 1 results were in the mid-upper zone of the range of values the various estimators gave and were substantially above the bootstrap results, renowned for being conservative (Magurran 2003).

Equation 2-1 Jacknife 1 estimator of species richness

$$S_{Jack1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right)$$

Where, S_{obs} = the cumulative number of species in all the samples within each development stage Q_1= the number of species that occur in one sample only, and m= the number of samples.

2.1.1.4 Statistical power

Another facet of the sampling design was to produce data with ample statistical power to avoid a Type II error when distinguishing between attributes of development stages, taking into account variability among samples within each stage. This is an important data-set property because the primary aim of data analysis is to examine change in assemblage properties among stages. For the Thomson and Godley sites (those sites sampled in the first season), this was not tested *a priori*. In the case of the Lake Thomson

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[3] Magurran (2003) recommends firstly that the family of nonparametric species richness estimators are the most effective because they are not based on the parameter of a species abundance model that has previously been fitted to the data, and secondly that the 'Jacknife 1' estimator has a good performance relative to others in the non-parametric family.

site, there were only five development stages available so all were sampled regardless of comparative dissimilarity. The Godley site development stages were not in contiguous zones and so had to be easily distinguishable from each other by eye; this was considered a sufficient test for statistical distinctness. In the case of the Fox Valley site (sampled in the second season), an attempt was made to estimate power *a priori* in order to optimise the trade off between number of samples versus number of stages sampled within the time available. This was done owing to the greater number of development stages potentially available to sample than at the other two sites. The method for this power test is described in the Fox site chapter (number five).

2.1.1.5 Plot locations

Criteria for plot locations were employed in all sites in order to reduce the variation of factors that may confound the inference of vegetation development gradients made with the chronosequence method. Owing to conditions being unique to each site, these criteria are listed in the methods sections of Chapters three, four & five. Where signal strength allowed, GPS coordinates were recorded for the centre of all plots in all study sites in case researchers in the future would wish to re-sample. Plot coordinates (in the New Zealand Map Grid format) are given with an accuracy range per site in Appendix two.

2.1.2 MEASUREMENT OF ENVIRONMENTAL VARIABLES

With the aim of characterising all of the key features of the physical environment, environmental data were recorded for each site. Measured variables common to all sites were altitude, slope and soft sediment depth. Altitude and slope were measured using an altimeter and abney level respectively. Aspect was only measured at the Lake Thomson site owing to it being the only site with enough slope to make aspect variability important in terms of solar radiation and exposure to weather conditions.

Soft sediment depth was recorded in five random positions within each plot by pushing a 70 cm long aluminium probe into the substrate as far as it could go. The mean of the five recordings was taken as the plot statistic. Each of the five recorded depths was itself a mean of three measurements taken within 10 cm radius of each other. Each measurement started at the base of the un-decomposed litter layer (i.e. directly above the organic soil horizon) and was made in an area free of subterranean wood and large rocks. Accurate measurement of soil profile depth is not possible using this method because a probe cannot reliably differentiate between soil and inorganic sediment. Probe

measurements are therefore termed as 'soft sediment depths' and whilst they cannot be used to ascertain absolute soil depth they are assumed to be approximately proportional to soil depth. Soil pits, the only reliable alternative method of measurement, were not permitted in any of the sites owing to National Park regulations.

2.1.3 SOIL SAMPLING FOR PH & ORGANIC CARBON

Soil samples were taken from Fox and Thomson sites only. The Godley site was omitted because of the lack of a developed soil profile in all but the final development stage.

Information about soil development is a useful complement to floristic data because it links the abiotic variables such as substrate texture and fertility with the biotic variables associated with vegetation community development (Matthews 1992). Organic carbon and pH were the two variables chosen to indicate soil development because they have been used successfully in many studies of primary succession for this purpose (Walker & del Moral 2003), and both are relatively easy to determine.

Taking standard depth samples from the surface zones of soil profiles is a robust way of sampling soils for comparison of pH and organic carbon across a range of different plant communities (Allen et al. 1986). Furthermore, the majority of soil chemical variability within a single soil-vegetation association occurs over distances as small as 10 cm (Allen et al. 1986). Therefore, in order to capture and average the chemical variability within each plot, 10 soil samples were taken from random positions throughout the plot. Each sample was taken from the top of the organic layer to a depth of 10 cm (or to the base of the soil profile if soil did not attain that depth) using a 25 mm inner diameter stainless steel soil corer. The corer was cleaned between samples and all samples were bulked, well mixed, double plastic bagged, labelled and frozen until analysis.

2.1.4 COVER ABUNDANCE ESTIMATION

In order to assess development of plant assemblages, abundance information for all vascular plant species was collected. Abundance measurements were made by way of cover estimation using a modified version of the 'reconnaissance description' (RECCE) methodology (Allen 1992). The RECCE method is widely used throughout New Zealand for describing compositional variation of vegetation assemblages, especially in forest ecosystems.

The RECCE method derives cover estimates by dividing the three-dimensional plot space into tiers. The number of tiers, as well as their depth and height were dependent on the physiognomic strata evident in each individual plot. Tier depth estimates represent the distance between the heights of the base of the tier above and the top of the tier below and were made using an abney level at a measured distance and trigonometric calculations. Each species is assigned a cover value for each tier in which it occurs, starting with the upper tier and working down through the tiers in sequence. Cover values represent the total cover of all individuals present per tier excluding their flowering or woody parts. Cover estimation guide sheets from the 'Global Observation Research Initiative in Alpine Environments' (GLORIA) field manual (Pauli et al. 2002) and the RECCE manual (Allen 1992) were used regularly to check the accuracy of observer visualisation. In addition, the ground area within each square plot was divided by tapes into four sub-units to aid cover estimation. A consistent search time was devised to suit each development stage of each site (one sufficient enough to discover most rare species) so that sampling effort remained reasonably even among replicates.

In order to give an abundance measure more representative of the relative abundance of each plant species within the sample, cover values per tier were multiplied by the tier depth and then values for each tier were summed. The result of this calculation shall be referred to as the 'importance score', a measure expressed in cubic metres.

Equation 2-2 Generic equation for the calculation of importance score per species per plot

$$I_i = \sum_{j=1}^{n} (ijHj)$$

Where I*i* is the importance score for species *i* in metres cubed, and *ij* is the cover abundance value in metres squared for species *i* in tier *j* for *n* number of tiers (dependent on individual plot physiognomy) and H*j* is the depth of tier *j* in metres.

In this study, two modifications have been made to the RECCE methodology. Firstly, the Braun-Blanquet cover scales (Braun-Blanquet 1951) were not used. Instead, for species with >1 % cover, they were replaced by a percentage cover figure to the nearest whole number[4], and for species with <1 % cover, by an area estimate in cm^2, as in Pauli et al. (2002), which was later converted into percentage cover. The reason for this modification is two-fold. Firstly, it increases the accuracy of the characterisation of the relative abundance distribution of each development stage. Secondly, discrete cover classes have been shown to have little application in diversity measurement (Magurran 2003) because their non-linear nature impedes comparisons and interpretation.

The second RECCE modification, applied in the forest sites only, was to estimate cover, rather than recording presence/absence only, for epiphytes. This was necessary to compare development stages using indices that require species abundance information for the entire plant assemblage. Epiphyte cover values were derived for non-woody species by estimating the number of trees in the plot supporting epiphytes, their cumulative trunk and limb surface area (via trunk/limb diameter and trunk height/limb length estimation), and the average depth of the epiphyte growth in a perpendicular plane to the trunk/limb surface (the epiphyte tier depth). In this way, each species received a cover value in cm^2 which could be converted into an importance score using the epiphyte tier depth. Woody epiphytes, epiphytic tree ferns, spreading lianas and trailing plants all had their cover recorded in the normal way in whichever physiognomic strata tier(s) they occurred in.

Very little published information exists on whether cover provides a good estimate of biomass, or, whether the choice of method of abundance estimation affects the results of common methods of plant community analysis. Data from one study (Chiarucci et al.

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[4] Whilst absolute precision of the percentage cover to the nearest whole number was difficult to achieve by visual estimation, it is supposed that the cover estimate accuracy would be higher using this method than if cover classes were used. It was found that observer accuracy could be increased through amassing field experience (in each type of habitat) by sampling dummy plots, and by avoiding deliberation when assigning each cover value.

1999) that provides evidence to answer both these questions, is however from one structurally simple community type only. Their results showed that for most species, cover and biomass is significantly correlated and there is little difference in the correlations due to different life forms. Also of interest is that the choice of abundance measure makes little difference to the results of rank-abundances, ordinations and species diversity indices calculations. Criticisms made by Chiarucci et al. (1999) on the utility of the cover estimation method for observing the shape of the relative abundance distribution (RAD) have been addressed in this study because cover was estimated continuously. Therefore, for the purposes of this study it is assumed that cover estimation provides an adequate measure of abundance for the analyses conducted, and, furthermore, that the importance score is a suitable proxy for biomass.

To provide additional characterisation of the development stages, ground cover percentages were estimated for each of the following classes: vascular plants, non-vascular plants, litter, exposed soil and exposed sediment. Ground cover is defined as what is visible from above.

2.1.5 PLANT SPECIES IDENTIFICATION

Plants were identified to species level[5]. If a plant could not be confidently identified in the field, a tag name was used and a voucher specimen was taken to enable later identification by consultation with field guides (Allan 1961; Moore & Edgar 1976; Wardle 1979; Webb et al. 1988; Brownsey & Smith-Dodsworth 1989; Poole & Adams 1994; Wilson 1994, 1996; Edgar & Connor 2000), herbarium specimens and botanic experts. Experts consulted include Dr. Aaron Wilton, Richard Ewans, Adrienne Markey, Associate Professor David Norton, Professor Colin Burrows and Chris Woolmore. Voucher specimens were taken from each plot where a particular tag name was used to ensure identification consistency, and, to build up a picture of the form and size variation of

[5] A few species were identified as a morphospecies if a species name could not be assigned to field samples (e.g. *Coprosma* sp.) whether the taxa concerned was poorly defined or not.

ambiguous or variable species. All specimens have been pressed, dried, arranged in scrap books and cool temperature treated to kill insects. Nomenclature follows the on-line New Zealand plant names data-base (Allan-Herbarium 2000) maintained by Landcare Research. Species lists for each study site are given in Appendices five, seven & eight.

2.2 ANALYSIS TOOLS

Table 2.1 summarises the analyses and calculations applied to data from all sites and details which data sets each used. The order of Table 2.1 mirrors the order of the following sections that detail the methods used for each of these analyses in turn.

Analysis method	Data set(s) used
Development stage plant assemblage description	
Plant assemblage compositional summary & naming	Species importance scores (including tier distribution information)
Multivariate analyses part one	
Ordination - correspondence analysis (DCA & DCCA)	Species importance scores & environmental data
Analysis of similarities (ANOSIM)	Species importance scores
Linear regressions (regression part one)	DCA axis one sample scores & environmental data
Calculation of univariate indices	
Soil acidity (pH)	Soil chemical analysis results
Soil organic carbon content	Soil chemical analysis results
Importance score (per plot)	Species importance scores
Species density (richness)	Species presence / absence
Species diversity	Species importance scores
Species evenness	Species importance scores
Distance from lognormal RAD	Species importance scores
Growth form diversity	Species presence / absence
Functional richness	Species presence / absence
Functional evenness	Species importance scores
Functional difference	Species importance scores
Taxonomic distinctness	Species presence / absence
DCA axis one	DCA axis one sample scores (derived from species importance scores)
Multivariate analyses part two	
Linear & polynomial regressions (regression pt two)	Univariate indices, development stage age estimates
Ordination - principal components analysis (PCA)	a) Species importance scores; b) Univariate indices

Table 2-1 Univariate and multivariate analysis methods with the data sets used for each.

2.2.1 EXPLORATORY DATA ANALYSIS (EDA) & DATA MANIPULATION

EDA is an important preliminary step in the analysis of vegetation data that familiarises the investigator with the data-set by exploring patterns and facilitates the generation of hypotheses to be tested by more advanced methods (Kent & Coker 1992). In this study EDA techniques were used to thoroughly examine the species and environmental data prior to conducting any analysis or index calculation. Data were assessed for possible data entry errors as well as to ascertain if any outliers in the species data were linked to variation of the environmental variables. No such outliers were found.

Once indices had been calculated, a second phase of EDA was undertaken to do the same for them. Furthermore, EDA techniques were used to examine the patterns within and relationships between variables which is important for the correct interpretation of correlation and regression results (Anscombe 1973; Zar 1999).

EDA techniques included making box and whisker plots of each variable against development stage as well as scatter plots of all variables against each other among logical sub-sets (environmental variables, univariate indices, floristic attributes). Three dimensional scatter plots were used to display any relationships between two variables of interest against development stage.

Finally, in order to meet the assumptions of multivariate analyses, transformations were made for environmental variables and indices whose values displayed a heterogeneity of variance among development stages. Transformations adopted vary between study sites and are detailed in the relevant chapter sections.

2.2.2 DEVELOPMENT STAGE PLANT ASSEMBLAGE DESCRIPTIONS

Each development stage of each site, despite variation among replicate samples, has a plant assemblage with a characteristic form, structure and composition. Three methods were used to characterise each assemblage: 1) a composition summary table, 2) a specific name and 3) a description. These methods are detailed in the following three sections.

2.2.2.1 Plant assemblage composition summary

For each site, a summary of development stage plant assemblage composition is given in a tabular form by detailing mean relative abundances per stage for common species. Relative abundances were calculated as the percentage of total importance per

sample that each species comprised. A common species was defined as one that exceeded a minimum percentage threshold in at least one development stage. The threshold varied among sites according to the species relative abundance distribution of each site so that the table included a manageable number of species.

2.2.2.2 Plant assemblage naming

Naming of development stage plant assemblages follows the system proposed by Atkinson (1985) for the mapping of vegetation units in Tongariro National Park, New Zealand and subsequently followed by others with minor modifications to suit the novel vegetation types encountered (e.g. Norton & Leathwick 1990). Modifications to Atkinson's system used in this study were: 1) scientific names used for the plant species, 2) growth forms defined using Druce's (Druce 1993) categories (See Appendix three for definitions), and 3) vegetation types named by their most abundant plant species regardless of how low the cover values of those species were.

The system uses a two-part name that refers to the compositional and structural characteristics for each development stage respectively.

The compositional name is derived from the names of the dominant and conspicuous species composing the vegetation as follows:

- All those species with ≥20 % of the total vegetation cover present in all tiers
- Where no species reached the 20 % level, the two most abundant species
- Conspicuous species, which frequently contribute less than 20 % of the canopy cover are included if their characteristic nature would render the name incomplete with no mention of them.

The range of percentage cover values of the species used in the compositional name is split into classes. Within each class, the species are quoted in order of decreasing abundance. The class identity is indicated by a system of underlining and brackets as follows:

- *Weinmannia racemosa* = ≥50 %
- *Weinmannia racemosa* = 20-49 %
- (*Weinmannia racemosa*) = 10-19 %
- [*Weinmannia racemosa*] = 1-10 %
- {*Weinmannia racemosa*}= <1 %

The second part of the name indicates vegetation physiognomic structure as determined by the most abundant growth form, or, where vegetation cover is exceeded by

bare substrate, by the dominant substrate type. The criteria for assigning the structural part of the name are detailed in Table 2.2 below.

Structural class name	Diagnostic criteria for structural classes
Forest	Woody vegetation in which the proportion of total cover that trees and shrubs comprise is ≥80 % and in which tree cover exceeds that of shrubs. 'Low' is attached to the name as a prefix if the mean canopy height is ≤10 m high.
Scrub	Woody vegetation in which the proportion of total cover that shrubs and trees comprise is ≥80 % and in which shrub cover exceeds that of trees
Tussockland	Vegetation in which the proportion of total cover that tussock forming grass species comprise is 20-80 % and in which the tussock cover exceeds that of any other growth form or bare ground.
Grassland	Vegetation in which the proportion of total cover that non-tussock forming grass species comprise is 20-80 % and in which their cover exceeds that of any other growth form or bare ground.
Stonefield / Gravelfield	Land in which the area of unconsolidated bare stones (20-200 mm ∅.) and/or gravel (2-20 mm ∅) exceeds the area covered by any one class of plant growth form. The name given depends on whether stones or gravel form the greater area of ground surface. Stonefield and gravelfield compositional names are derived from the leading plant species, regardless of how low the cover values are.
Rockland	Land in which the area of residual bare rock exceeds the area covered by any one class of plant growth form. The compositional name given is from the most abundant plant species regardless of how low the cover values are.
Mossfield	Vegetation in which the proportion of total cover that mosses comprise is 20–100 % and in which the moss cover exceeds that of any other growth form or bare ground.

Table 2-2 Diagnostic criteria for assigning development stage vegetation structural classes. Adapted from Atkinson (1985).

Structural information, in addition to that provided by the structural class name, was incorporated within the compositional name by using hyphen (-) and diagonal sign (/) symbols to convey tier height relationships between the species; hyphens link species whose major component of cover occurred in the same tier, and, diagonal signs link species whose major component of cover existed within different tiers. Those species with most of their cover in higher tiers are quoted before those with most of their cover in lower tiers even if their total cover maybe less than a species quoted afterwards.

2.2.2.3 Plant assemblage descriptions

The plant assemblage descriptions attempt to convey the visual impressions and main botanical components that an ecologist with local knowledge would notice. The descriptions draw from field notes and field sheets as well as the tiered cover abundance species data.

2.2.3 MULTIVARIATE ANALYSES PART ONE

The ordination, ANOSIM and stepwise linear regression methods that follow are employed to investigate thesis question **I:** *How do floristics vary with age and does the main floristic gradient correlate more closely with age than any other environmental variable* ?

The latter half of thesis question one is posed in order to check that the chronosequences sampled in the three case studies were robust enough to allow the assumption to be used that the floristic gradient among development stages represents a time gradient. As the question suggests, it must be proved that environmental variables are far less important than age in explaining floristic variation. The correspondence and regression analyses employed are considered to be amply able to do this. These methods do not test that all environmental variables are invariant among development stages but this is not the question of interest and, furthermore, it would be unrealistic to expect that such constancy would be so in all cases. Previous authors have also taken the pragmatic approach that using data from a chronosequence is warranted if floristic differences can be shown to be due primarily to age of surface, rather than only if age is the sole environmental factor which varies (e.g. Pickett 1989; Fastie 1990). Therefore, in order to investigate the questions tested by this thesis it is considered unnecessary to test for statistically significant variance of environmental variables among development stages; either on a pair-wise basis or among all stages.

2.2.3.1 Ordination – DCA & DCCA

For all three sites separately, the parametric[6] ordination methods of Detrended Correspondence Analysis (DCA) and Detrended Canonical Correspondence Analysis (DCCA) were used to describe the pattern of floristic variation among all the samples as well as to assess relationships between sample floristics and measured environmental variables. Version 4.0 of the computer program CANOCO[7] (ter Braak & Smilauer 1998) was used to compute the ordinations.

Default options were used in the analyses, except that the downweighting option for rare species was chosen so as to reduce any disproportionate effect they may have (ter Braak & Smilauer 1998) on the ordination diagram. No transformations of any of the species data sets was necessary because the distribution of the species abundances were not highly skewed (Jongman et al. 1995). Transformations of environmental variables varied among the three data sets. Environmental variables included in the DCA & DCCA analyses also varied among sites and are presented in the relevant chapters. No standardisation of any environmental variables (for measurement on different scales) is necessary for correspondence analysis owing to its use of non-linear unimodal models (ter Braak & Smilauer 1998).

DCA provides an indirect ordination of the species-by-plot data matrix, identifying the dominant gradients of floristic variation independent of other factors, e.g. environmental variables (Jongman et al. 1995). Each axis maximises the dispersion of the species scores subject to the constraint that it is uncorrelated with the previous axis. Therefore, each axis represents an independent floristic gradient. Sample scores for each axis are derived by calculating weighted averages of the species scores for each axis within each sample. The first four axes are expected to explain most of the variation that is

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[6] Correspondence analysis is based on multiple regressions.

[7] Multidimensional scaling (MDS), a non parametric type of ordination offered in the PRIMER package (Clarke & Gorley 2001b) was tested on all three data sets. Patterns were found to be no better than those achieved with the correspondence analysis. Therefore, the parametric correspondence analysis offered by the CANOCO package was chosen in favour of MDS because of its useful quantitative outputs.

'important' (i.e. that which is not random noise). The first two axes generally explain the majority of the variance explained by the first four. Therefore, a two-dimensional graph of DCA axes one and two scores is usually sufficient to illustrate the main pattern of floristic variation among and within development stages.

DCA also provides 'inter-set correlation' values for each environmental variable with each axis. These provide information on the importance of each measured environmental variable in explaining the variation of species data. This enables the confounding effect of included environmental variables upon the inference of successional pattern drawn from the chronosequence data to be assessed. However, the calculation of the correlation coefficients behind the inter-set correlation values does not take into account any colinearity that may exist between variables (ter Braak & Smilauer 1998) included in the analysis (e.g. age). Therefore, a correlation may be misleadingly high for an environmental variable if it partially represents the variables' correlation with floristic variation due to age as well as its own effect on floristics. For this reason any environmental variables other than age that inter-set correlation values suggest to have an effect on floristics (either DCA axis one or two gradients) are tested with stepwise regression methods to quantify the significance of their unique effect.

In contrast to DCA, DCCA is a direct ordination that extracts the dominant gradients with the constraint that they must be orthogonal linear combinations of independent (environmental) variables (ter Braak 1996). Variance Inflation Factors (VIF's) in the computation outputs were used to check for levels of multicolinearity of environmental variables (ter Braak & Smilauer 1998) that may affect the validity of the DCCA analysis (or the interpretation of the DCA inter-set correlations mentioned previously). By correlating the constrained axis scores of DCCA with the unconstrained axis scores of DCA, it is possible to quantify the extent to which the measured environmental variables are driving the change in floristics described by the derived axes of DCA. If the correlation is high, then it can be assumed that there remains little un-measured environmental variation of importance to plant species abundance patterns. This facility complements the inter-set correlation values to give an extra degree of confidence that the vegetation development inferred by each chronosequence is unconfounded by environmental variation.

2.2.3.2 Analysis of similarities (ANOSIM)

It is a logical continuation from ordination to show that the floristics of each development stage is statistically different from its predecessor and successor (despite the considerable variation among replicate plots owing to natural spatial heterogeneity) for each chronosequence. It is fundamental to show such a difference between stages because if it were not the case, it would be very difficult to justify pursuing the key thesis objective of analysing and comparing univariate index response trajectories to vegetation development. Use of the parametric multivariate analysis of variance method was rejected. This was because the method's assumption that the probability distribution of species abundance data is approximately normal could not be met by any transformation, owing to the dominance of zero values in species abundance data (Clarke & Warwick 2001). Instead, the non-parametric ANOSIM procedure of the PRIMER package is used because this has no such assumption.

In the ANOSIM procedure the Bray-Curtis similarity coefficient (Bray & Curtis 1957) is computed for all samples based on the untransformed species abundance data. These similarity coefficients are subsequently used to create a pair-wise similarity matrix for all samples.

$$B = \frac{\sum_{i=1}^{n}(x_{ij} - x_{ik})}{\sum_{i=1}^{n}(x_{ij} + x_{ik})}$$

Equation 2-3 The Bray-Curtis similarity coefficient (B) where X_{ij}, X_{ik} = the number of individuals in species i in the samples j and k, and where n = the number of species in a sample. This similarity coefficient ignores cases in which the species are absent from both community samples and is dominated by the abundant species, such that the importance of rare species is down-weighted.

The similarity matrix is used to compute a test statistic, 'R', which reflects observed differences between surfaces contrasted with differences among each surface's replicates. The significance level of R is calculated by referring the observed values of R to the simulated permutation distribution for R with the number of samples concerned under the null hypothesis of 'no stage differences'.

Equation 2-4 Calculation method for the R statistic in the ANOSIM procedure.

$$R = \frac{\left(\bar{r}_B - \bar{r}_W\right)}{\frac{1}{2}M}$$

Where $\bar{r}_W$ is the average of all rank similarities among replicates *within* stages and $\bar{r}_B$ is the average of rank similarities among all pairs of replicates *between* stages and $M = n(n-1)/2$ and n is the total number of samples under consideration.

2.2.3.3 Regression (part one)

The two main questions pertaining to each of the three data sets that regression analysis was used to investigate were:

1. Do any of the environmental variables that were either not included in correspondence analysis or that were significantly correlated with an ordination axis explain a significant amount of the main floristic gradients when considered alone or in combination?
2. Are values of univariate indices dependent on age and if so does a linear or polynomial model fit the response pattern best?

The two regression procedures, followed identically among study sites, used to answer these two questions respectively were:

1. Linear stepwise regressions of multiple environmental variables against gradients of floristic variation with the variation explained by age taken account of
2. The sequential fitting of linear & second order polynomial regression models to the response of each index to age

To retain the logical order of data interrogation followed in the thesis, the two regression procedures are split between two sections. In order to retain their link with ordination, the methods for the procedure testing the first question are covered in this section, so too are the generic methods pertaining to both procedures. Whereas, the methods for the procedure testing the second question are covered in regression part two (Section 2.2.5.1.) after the calculations of the indices concerned are detailed.

In addition to these two standard procedures there are other uses of regression in this thesis. Firstly, there are slightly variant stepwise methods used in Chapter five because of issues with environmental variable measurement in the Fox Valley site. Secondly, a

more complex regression procedure is followed to analyse similarity of index response trajectories to age among study sites in Chapter six. Methods for both these procedures are described in the respective chapters.

2.2.3.3.1 General methods that apply to all regression procedures used

The GenStat package was used to conduct all regression analyses via the command language. Scripting was aided and reviewed by my statistics advisor, Dr. R. Littlejohn. Initially, a trial run was used to generate graphs of the standardised residuals of all variables fitted to age on a $\log_{10}$ scale. These graphs were scrutinised for extreme outliers with large residuals or for patterns in residuals and also to assess the need for data manipulations to satisfy the assumptions of regression analysis. Regression analysis relies on the assumption of homogeneity of variances among groups of samples (Zar 1999); this was met via two methods of data manipulation. Firstly, transformation was performed on only the variables that displayed a functional relationship between value and variance. Variables requiring transformation were different among the three data sets so are detailed in the individual study site Chapters' regression sections (3.3.3.5, 4.3.3.6, 4.3.3.8, 5.3.3.5). Secondly, following the transformation step, the homogeneity of variances among the data groups for each stage was quantifiably assessed for each variable by computing Bartlett's test (Bartlett 1938). A 'pass' result for Bartlett's test, meaning homogenous variance, was set at the critical value of ≥ 0.01 because ≥ 0.05 was deemed to be not stringent enough considering the chances of a type I error with the high number of degrees of freedom involved. All variables that passed were subjected to a non-weighted regression. All variables that failed were subjected to a weighted regression where an individual weight was applied to each stage's data points that was proportional to the difference of their variance from the pooled variance for the whole data set. The weights were automatically calculated by GenStat from the standardised residuals.

A further analysis run was then made with the transformed and weighted variables. Outputs from this run were screened for error messages regarding data points with large residuals or high leverage. Outlying data points with large residuals were considered to be acceptable if their leverage effect was low; those with high leverage were removed. A final run was then made from which the results were taken.

2.2.3.3.2 Linear stepwise regression

The general strategy employed was to model DCA axis one and two with the selected environmental variables, with age added as a fixed variable (i.e. one that is fitted without the option of being dropped) to take account of the variation it explains. To add the environmental variables, a stepwise multiple regression procedure available in the GenStat package was adopted. The procedure adopted involves sequential addition by forwards selection, and, optional subsequent elimination of input variables. Elimination takes place if the inclusion of the variable in the model reduces the residual mean square (RMS) of the model by less than a critical amount (which is by default set at a negligible non-significant level). The selection or elimination decision is made each time an additional step in the procedure is taken by examining the partial regression coefficients for all variables in the model. Therefore, the elimination of an added variable can take place immediately upon its addition or subsequently once the effects of other variables are included in the model. Additional steps were made until no further change to the variables in the model took place.

2.2.4 UNIVARIATE INDICES OF VEGETATION DEVELOPMENT

The univariate indices that follow are those that are referred to in thesis questions two and three: **II** *Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?*

III *Which indices have strong and consistent responses to all three case study vegetation development gradients; i.e. which of the tested indices have predictable enough responses to be suitable for the evaluation of restoration success via trajectory analysis?*

Univariate indices allow the response trajectories to vegetation development of the parameters they measure to be easily presented and analysed. Moreover, these indices also facilitate comparisons to be made between the responses to the different development gradients that occurred at the three sites studied (see Chapter six). The 13 indices used in this study relate to seven aspects of plant assemblage structure and ecosystem function: soil chemical properties, plant biomass, plant species diversity, plant assemblage fit to RAD models, plant functional diversity, plant taxonomic diversity and plant species turnover. All these aspects have been reported or perceived in the literature to be sensitive

to successional gradients. The selection of individual indices to measure is based on the philosophy that they should have practical applicability to person(s) assigned the task of measuring the success of a restoration project, taking into account their likely objectives, workload and expertise. As a whole, the suite of indices chosen are designed to have a high level of complementarity in terms of the aspects of the plant assemblage structure measured.

The following sections detail the methods of calculation for each univariate index. In addition, a summary of the ecological information conveyed by each index is provided to give a background to the interpretation of index responses given in Chapters three, four, five & six.

2.2.4.1 Soil chemical properties

Whilst soils and soil properties are a driving mechanism for vegetation change (e.g. Burrows 1990), and indeed have been shown to have a profound effect on a forest succession similar to that of the Fox study site (Richardson et al. 2004), the aims of this study are not to isolate the mechanisms of change; they are simply to assess indicators of that change. Therefore, in this study soil properties are treated as an indicator of vegetation development, and the fact that their response to successional gradients is a well studied phenomenon facilitates interpretation.

2.2.4.1.1 Organic carbon – loss on ignition method

Methods followed Allen et al. (1986). Soil was air dried at 40°C until weights of the samples were stable. Approximately two grams of sieved (≤2 mm) dried soil was placed in crucibles in a muffle furnace for two hours. Samples were allowed to reach 550°C from room temperature to avoid deflagration. Samples cooled in a desiccator to room temperature were re-weighed to calculate the 'loss on ignition' (LOI) percentage of organic matter. The correlation between organic matter and organic carbon for non-

calcareous soils (Ball 1964) was used[8] to convert the LOI organic matter percentage into an estimate of the percentage organic carbon.

2.2.4.1.2 pH

Methods followed Allen et al. (1986). Four grams of air dried sieved (≤2 mm) soil mixed with 50 ml of distilled water was shaken for 15 minutes and left to stand for 20 minutes. Readings from a digital pH meter were recorded after 30 seconds of immersion in the gently stirred soil solution. The electrode was washed with distilled water between each sample. Calibrations of the pH meter were made with buffer solutions of pH four and seven, and repeated after every twenty samples. Temperatures of all samples and buffer solutions were equalised to room temperature prior to measurement.

2.2.4.2 Sample importance score

The calculation of the importance score per species is explained in section 2.1.4. The sample importance score is simply the sum of all the importance scores for its constituent species. Because the species importance scores are calculated from data derived with the same standard RECCE method (Allen 1992), the sample importance scores can be directly compared between samples of the same development stage, different development stages, or different study sites[9].

2.2.4.3 Species diversity indices

Three indices were chosen which represent three different aspects of species diversity; species richness, dominance and evenness. Indices to represent the dominance and evenness aspects of species diversity were chosen *a priori* using the following criteria; their range of values have intuitive meaning, they are less sensitive to sampling intensity of assemblages, and do not have problems of unstable variance. Index selection using *a priori*

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[8] The ratio of organic matter to organic carbon published by Ball (1964) is 0.58.

[9] A multiplication factor was required in order to make plot importance scores between the grasslands and forest sites comparable (so as to compensate for the difference in plot size between the two ecosystem types).

criteria is preferable to selection on the basis of, for example, differentiation of results among development stages (Magurran 1988). Simpson's diversity (D) and Simpson's evenness ($E_{1/D}$) are used to represent the dominance and evenness aspects of species diversity respectively, they are both 'non-parametric'[10] statistics (Magurran 2003).

The Shannon index, a very commonly cited and used index of species diversity, is not used in this study because many of the references consulted that discuss the merits of different diversity indices recommended against its use (May 1975; Magurran 1988; Lande 1996; Magurran 2003) owing to its sensitivity to sample size and narrowly constrained value range making interpretation of assemblage comparisons difficult.

There is a lack of knowledge on how aspects of species diversity affects ecosystem processes and vice versa (Ehrenfeld & Toth 1997). The relationship between species richness and ecosystem functioning is inconsistent (Naeem 2002; Naeem & Wright 2003; Hooper et al. 2005). It has been thought for some time that the link is via functional diversity (Tilman et al. 1997), either through the presence of important traits or the range of traits present with the assemblage (Diaz & Cabido 2001; Hooper et al. 2005). Thus, the cases where species richness acts as a surrogate for functional diversity are limited to when functional coverage is linearly related to species richness (Diaz & Cabido 2001). Recent models indicate that species richness provides resilience and stability in ecosystem functions but reduces population stability (Chapin et al. 1997; Gunderson 2000), however again this may be related to the functional diversity within the species assemblage (Walker et al. 1999).

2.2.4.3.1 Species 'density' (species richness)

In this study species richness is measured by the number of species per sampling unit (the 10 x 10 or 5 x 5 m plot), a common definition for botanical studies (Kent & Coker 1992), and is hereafter referred to as 'species density' (Magurran 2003). This naming is

[10] Non-parametric in this case means that the indexes are not explicitly associated with any statistical models of the underlying species relative abundance distribution (Magurran 2003).

used to avoid confusion with absolute species richness ('S_{max}'), (*sensu* Colwell & Coddington 1994; Magurran 2003). S_{max} is defined as the theoretical maximum richness in an entire species assemblage; in this study referring to the entire extent of each development stage.

Values of species density are notoriously sensitive to variation in sampling effort (Magurran 2003) and as such it can be a problematic measure for comparing distinct species assemblages with. Sampling effort among samples was homogenised by employing standard search times. Furthermore, the sampling effort sections for each study site (Chapters three, four and five) show variation in cumulative effort among development stages to be acceptable for the use of species density as an index with which to compare the development stages in all sites.

2.2.4.3.2 Species diversity (*D*)

Simpson's diversity index (*D*) (Simpson 1949) is a heterogeneity measure that captures the variance of the species abundance distribution and is partially dependent on species density (Magurran 2003). It is heavily weighted towards the most abundant species in the sample (Magurran 2003), hence as *D* increases, the extent to which a few species dominate increases.

The form of the index for a 'finite' assemblage, such as that represented by a fixed-dimension sample, is:

Equation 2-5 Equation used to calculate Simpson's diversity index (*D*).

$$D = \sum \left[\frac{n_i[n_i - 1]}{N[N-1]} \right]$$

where n_i= the abundance of the *i*th species in the sample; and *N*= the total abundance of all species in the sample.

In this study, the index is expressed using the natural log transformation (-ln(*D*)) after Pielou (1975) to avoid variance problems following the recommendation of Rosenzweig (1995). Also, when expressed in this way, the index values vary more intuitively, whereby an increase corresponds to an increase in diversity (and a decrease in dominance by a few species).

2.2.4.3.3 Species evenness ($E_{1/D}$)

In contrast to Simpson's diversity, Simpson's evenness (Smith & Wilson 1996) is independent of species density; it is therefore considered a pure evenness measure (Magurran 2003). Thus, Simpson's evenness does not behave as the reciprocal of Simpson's diversity, although the concepts of evenness and dominance are opposite.

Simpson's evenness ($E_{1/D}$) is calculated by dividing the reciprocal form of the Simpson's dominance index by the number of species in the sample:

Equation 2-6 Equation used to calculate Simpson's evenness.

$$E_{1/D} = \frac{(1/D)}{S}$$

where S is the number of species in the sample and D is Simpson's diversity index.

The measure ranges from 0-1, where 1 represents absolute evenness of all species abundances within the sample assemblage.

2.2.4.4 Distance from the lognormal model of species relative abundance distribution (ΔL)

A normalised χ^2 test for goodness of fit statistic ('ΔL') is used to examine whether distance from the lognormal model of species 'relative abundance distribution' (RAD) changes along the successional gradients. Methods for this are described in the following sub-sections.

In addition to calculating this statistic, 'rank/abundance' plots ('dominance/diversity' curves *sensu* Whittaker (1965)) per development stage are presented to give a standard representation of the RAD. Rank/abundance plots are not specifically related to any distribution models. Therefore, they can be used to assess best fit among different RAD models by eye to aid interpretation of the assemblage changes along the successional gradient relative to the lognormal model (Magurran 1988; Wilson 1991) that are inferred by the ΔL statistic. In addition, studying the shift in rank/abundance plots among stages is useful for understanding the patterns of species diversity statistics based on proportional abundance because the RAD underlies such statistics. The shape of the RAD can shed light on the biological processes occurring during succession owing to the links models make between relative abundance shifts and niche apportionment (Tokeshi

1993; Magurran 2003). For these reasons rank/abundance plots are recommended as a first step to analysing species abundance data (Krebs 1999).

2.2.4.4.1 Calculation of the chi squared (χ^2) statistic

The chi squared (χ^2) test of the fit of the RAD to the lognormal distribution was calculated using GenStat[11]. The species importance score data matrix was converted into a matrix of species counts per percentage abundance class, or, 'octave' (*sensu* Preston (1948)), where octaves were derived by log base two and a spare octave of zero values was left at either end. The zero values are present to provide a stop command to the algorithm. This method of fitting is appropriate for non-truncated distributions (i.e. one without a 'veil-line', *sensu* Preston (1948)) such as all complete assemblage plant abundance data sets have (Wilson 1991), because their highly plastic biomass effectively means there is no lower limit to the abundance of a species in an assemblage. Finally, a χ^2 test per sample was performed on the observed species per octave frequency distribution against the expected lognormal model of distribution.

2.2.4.4.2 Suitability of the χ^2 goodness of fit test for the data

For many decades, the χ^2 goodness of fit method was not considered suitable for testing data with an expected value of less than five in any octave (Zar 1999). Unfortunately, this condition would be violated for almost all samples for all sites studied in this thesis because of the number of octaves required to accommodate the abundance range of observed data (using a log base of two to derive them[12]) and the low levels of observed species density. However, Zar (1999) cites work showing the χ^2 test to be robust

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[11] GenStat uses the 'poisson', or, 'discrete' method to fit the lognormal distribution, where it is assumed that the continuous lognormal is represented by a series of discrete abundance classes (octaves) which behave as compound poisson variates.

[12] To ameliorate this problem, frequency classes derived using log base four were trialled, but, a quick glance at the resultant frequency class abundance distribution graphs showed a loss of too much information considering the purpose of the test. In any case, Zar (1999) recommends avoiding such data manipulations.

for situations where the number of octaves is more than three and the number of species observations is more than ten. This would apply for almost all of the samples in this study. Stephens (1974) reviewed the performance of goodness of fit tests that use statistics based on the empirical distribution function (EDF) in comparison to χ^2 (including the Kolomogorov-Smirnov test). Stephens found that although the EDF statistics had appreciably more power than χ^2, they were not as robust at the relatively low level of observed species numbers that characterises the assemblages in this study.

2.2.4.4.3 Modifying the χ^2 statistic to give a distance from fit , ΔL.

Having accepted that the use of the χ^2 statistic is appropriate for testing goodness of fit, there is a further issue to resolve. The χ^2 statistic in its standard form is inadequate to examine the distance from the lognormal distribution because it simply gives a statistic for the mathematical likelihood of each sample fitting that distribution within a given probability (Stephens 1974). Indeed, Hughes (1986) asserts that such goodness of fit tests are notorious for having low discriminatory power. Unfortunately, most ecological workers dealing with the lognormal distribution have simply stated whether or not the data fit (usually using either the Kolomogorov-Smirnov or the χ^2 test) and given the specified significance level (Halloy & Barratt 2001). Therefore, in the absence of any well recognised method with which to quantify the departure from the lognormal distribution pattern, an attractively simple way suggested by Halloy & Barratt (2001) is used. The method standardises the χ^2 value through dividing it by the number of species (n) in the sample to give the 'normalised sum of squares differences' (ΔL) statistic. The value of ΔL decreases with decreasing distance from the lognormal distribution.

2.2.4.4.4 Interpretation of the ΔL statistic

Applying the ΔL statistic to primary successions of different ecosystems enables the investigation of the commonly held theory that the RAD of undisturbed assemblages approximates the lognormal pattern and that, following perturbation, assemblages tend to a less lognormal distribution, returning to the lognormal during recovery from perturbation (Preston 1962; Patrick 1963; Frontier 1985; Kevan et al. 1997; Halloy & Barratt 2001; Halloy & Whigham 2005). Sugihara (1980) developed a biological model to explain the lognormal distribution based on niche apportionment/filling, where successive niche creation events within a system gradually produce a distribution closer to the lognormal. However, this view has not gone unchallenged with some authors preferring to explain the

prevalence of the lognormal distribution as simply a statistical artefact of large data-sets related to the 'central limit theorem' (May 1975; Ugland & Gray 1982). More recently, explanation of the lognormal pattern has drawn on complex systems theory where a 'self-organised' system (one in which internal interactions are of greater importance to system functioning than external forces such as environmental factors or disturbances that are within their normal range (Halloy 1998)) displays the lognormal pattern as an emergent property indicative of having reached a self-organised state (Halloy & Whigham 2005).

2.2.4.5 Functional diversity indices

Functional diversity has been identified as possibly the most ecologically relevant biodiversity measure (Diaz & Cabido 2001), as it is an important determinant of ecosystem processes and functions (Grime 1998; Diaz & Cabido 2001; Loreau et al. 2002). It has been shown to be related to productivity (Tilman 1999), resilience (Nystrom & Folke 2001) and the inhibition of exotic species invasions (Prieur-Richard & Lavorel 2000). As such, I consider it not only likely to be sensitive to vegetation development after disturbance, but also to be relevant to the ecosystem function aspect of restoration goals. However, Diaz and Cabido (2001) caution that few diversity/ecosystem functioning studies have been undertaken with natural communities.

Despite its many plaudits, there is no consensus in the ecological literature about what functional diversity is, and no standardised measure for it (Hector et al. 2001; Lawler et al. 2001; Tilman 2001). Functional diversity in this study refers to the definition given by Tilman (2001, p. 109); "the value and range of those species traits that influence ecosystem functioning". In the past, functional diversity has been primarily derived by using either the values of functional traits for each species of an assemblage (e.g. Walker et al. 1999; Petchey & Gaston 2002), or the number of functional groups represented by species in an assemblage (Hooper 1998; Diaz & Cabido 2001; Tilman 2001).

This study assesses functional diversity using two traits; growth form and leaf area, the first being used to form functional groups to calculate one index and the latter being measured on a continuous scale to calculate three indices.

2.2.4.5.1 Shannon's growth form diversity

Growth form is a plant trait that is simple to measure. It is widely used to characterise changes in plant assemblages during succession with dominant growth form or growth form richness often used as the indicator metric (Bazzaz 1996; Walker & del Moral

2003). In this study, the Shannon diversity index (Shannon & Weaver 1949) is applied to the data where growth form category replaces species identity in the standard calculation to provide a simple measure of the growth form diversity present[13].

Equation 2-7 The Shannon index applied to growth form data.

$$H' = \sum p_i \ln p_i$$

where p_i is the proportion of cover abundance found in the ith growth form category.

The index provides a way of analysing shifts in morphology, useful because such shifts can correlate well with response to disturbance (Lavorel et al. 1997). The PRIMER package (Clarke & Gorley 2001b) was used to calculate values for the index using the 'log-e' option.

Raunkiaer's life form classification system (Raunkiaer 1934) was considered for use but was rejected because major novel research would be required to categorise the New Zealand flora beyond the first hierarchical level of the system. The utility of applying the first level of the system to the data is limited because there are only five groups and most species within a forest or grassland ecosystem would fit into only one. Instead, the closest approximation to a life form classification for the New Zealand flora that exists (that of Druce (1993)) is used whereby categories are partially growth form and partially phylogenetic groupings of species. Minor modifications were made (see Appendix three) to Druce's growth form categories (as have other users; e.g. de Lange et al. (2004)) to result in 16 categories, rather than the original 14.

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[13] Magurran (1988) recommends the use of the Shannon index for calculating diversity in cases where the data is in the form of abundances for categories such as growth form or physiognomic strata, whereas she does not recommend its use for species abundance data.

2.2.4.5.2 Leaf area based functional diversity indices

The use of a single trait to measure functional diversity

All three of the following functional diversity indices are designed to be calculated from species abundance data combined with measurements on a continuous scale of any single species trait deemed to be functionally important. The use of trait(s) measured on a continuous scale to calculate functional diversity is widely considered to be an improvement over the use of an arbitrary scale of functional significance necessary for the formation of synthetic functional groups that were characteristic of early functional diversity measures (Petchey & Gaston 2002; Mason et al. 2003; Petchey et al. 2004). The use of a single trait, whilst it limits the breadth of ecosystem functions linked to the index, obviates the need for exhaustive work to obtain multiple trait values, as is the case for the commonly cited 'FD' index devised by Petchey and Gaston (2002) for example. Paradoxically, the number of functional traits used to derive Petchey and Gaston's 'FD' measure is probably the cause of its linear relationship with species richness shown in tests of index behaviour in natural plant systems (Petchey & Gaston 2002). Because of this linear relationship, it has no utility.

Why use leaf area?

It follows from the above discussion that if a single trait is used for functional diversity calculation, an important consideration is to select a trait linked to the ecosystem process of interest (Magurran 2003), in this case succession. In this study the morphological trait leaf area is chosen. Leaf area is a trait which is sensitive to environmental conditions (Halloy & Mark 1996; Cornelissen et al. 2003). It is therefore likely to respond to ecosystem perturbation in terms of the values selected for by conditions prevailing upon successional plant assemblages. Leaf area is an important factor in the physiological functioning of plants and thus affects the efficiency of plant mediated ecosystem processes. For example, Gates (1980) cites experimental evidence for

productivity to be dependent on leaf area. Furthermore, Diaz and Cabido (2001) linked leaf area to ecosystem processes such as productivity, biomass turnover and nutrient cycling as well as to structural complexity. They also showed it to be a significant explanatory variable for the separation of plant community types along a climatic stress gradient. In addition, a comparison of 24 plant traits found leaf area to be well correlated with 'specific leaf area' (SLA)[14] (Diaz & Cabido 2001). SLA itself is a widely used trait in functional diversity studies that is linked to the establishment, strategy, persistence and disturbance response of plant species (Weiher et al. 1999).

Estimation of leaf area

For this study, the definition of a 'leaf' follows Halloy (1990, page 294) as "any photosynthetic lamina (leaf, leaflet, or phyllode[15]) that is connected by ≤38 %[16] of its length with another lamina". Thus, if a photosynthetic lamina is connected by >38 % it would be a lobe of a larger leaf.

Mean leaf area per species was estimated from width, length and shape dimensions. Where possible, leaf dimensions have been measured directly from reference samples collected as being of average size per study site. The vast majority of species' leaf dimensions were derived from reference samples collected in this way (Thomson 92 %, Godley 90 %, Fox 97 %)[17]. Samples taken were of undamaged mature leaves, except for

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[14] Not used in this study because in view of the selection criteria for univariate indices of vegetation development, the extra time investment required to calculate SLA (involving the derivation of an estimate of average leaf mass per species) was not deemed to be justified by the extra information it may provide.

[15] The species of the *Carmichaelia* genus (*C. australis* & *C. arborea*) are the only species encountered in this study which use parts other than the leaf/leaflets (the stem) to perform a significant amount of their photosynthesis. However, it is not practical to measure the stem area, and, the species concerned are two of the most leafy species of the South Island Carmichaelias, so leaf area is used.

[16] This number corresponds well with an intuitive appreciation of the natural proportions of objects that are separate entities; it is obtained from the 'Fibonacci series' (Halloy 1990).

[17] It is noted that there was considerable variation in the leaf dimensions for the same species among study sites.

dimorphic species where the juvenile form was the most common and abundant form present (e.g. *Pseudopanax crassifolius*). For species without adequate collected reference material, leaf dimensions were taken as the median of the value range given in the Flora of New Zealand (Allan 1961; Moore & Edgar 1976; Webb et al. 1988; Edgar & Connor 2000).

The Fox Valley site reference samples consisted of five average sized leaves from five separate individuals of each species, whereas the other study sites samples were less numerous and were typically from one or two individuals. This extra degree of accuracy for one study site is a result of the decision to use leaf area as a character being made after the first season of fieldwork, during which the first two study sites were visited.

In order to convert the measured leaf dimensions (length and width at widest point) into an estimate of the leaf area, the pressed and dried leaf specimens for each species were classified into one of six leaf shape types that are described by formulae and descriptive terms given in Table 2.3 overleaf. Thus, each leaf area figure corresponds to a mathematical approximation[18] of the specimen's real shape.

This study tests the response of three recently published indices that aim to measure the following three components of functional diversity; 'functional richness' (Mason et al. 2005), 'functional evenness' (Mouillot et al. 2004) and 'functional difference' (Mason et al. 2003). To my knowledge, none of these indices have been tested either using leaf area information *per se* or against successional gradients. The first two indices, functional richness and functional evenness, encapsulate the same properties of functional diversity as species richness and species evenness do for species diversity (provided sections of the range in functional trait value are thought of as an analogue to species). Functional difference relates to the dispersion of abundance within an assemblage in terms of functional trait value.

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[18] A method of measuring leaf area by means of a scanner and specialist software was trialled but found to be very time consuming and no more accurate than the mathematical approximation method owing to the scanner tending to not resolve leaf margin detail and the difficulties of dealing with pressed specimens.

Leaf shape type #	Leaf shape type formula	Leaf shape type description
1	$LA_1 = \frac{(l \times w)}{1.2}$	Rectangle, tapering or rounded
2	$LA_2 = (w \times \pi) \times \left(\frac{l}{1.8}\right)$	Cylindrical
3	$LA_3 = \pi \times \left(\frac{l}{2} \times \frac{w}{2}\right)$	Ellipse
4	$LA_4 = \pi \times \left(\frac{\frac{l}{2} \times \frac{w}{2}}{1.2}\right)$	Ellipse, reduced by narrowing, tapering or dents/serrations
5	$LA_5 = \frac{(l \times w)}{1.5}$	Triangle, wide
6	$LA_6 = \frac{(l \times w)}{1.8}$	Triangle, tapering

Table 2-3 Table showing the formulae and descriptive terms (after Halloy 1990) that describe each of the leaf shape types used in the calculation of leaf area estimates, where LA_i = Leaf Area for the ith type, l =leaf length and w= leaf width at the widest point.

The three indices are characterised and calculated according to the descriptions in the following three sections.

Functional richness

Functional richness FR_{ci} (Mason et al. 2005) is the amount of functional trait space occupied by all the species within an assemblage and is independent of species richness. It is analogous to the concept of species richness in the sense that the functional space encompassed is considered regardless of the amount of biomass that occurs within it.

The index is derived by finding the proportion of the global range of the trait value (defined in this study as the total range existing among all the development stages within each study site) which exists within each species assemblage. In this way the index is standardised to enable comparison of different traits and assemblages with different global ranges of traits (Mason et al. 2005).

Equation 2-8 Equation used to calculate functional richness

$$FR_{ci} = \frac{SF_{ci}}{R_{ci}}$$

Where: FR_{ci} = the functional richness of functional trait c in assemblage i, SF_{ci} = the range of functional trait values encompassed by each species assemblage and R_{ci} = the absolute range of the trait (in this case R_{ci} *is* fixed as the observed range for the trait among all samples from all development stages).

Two disadvantages of this index were identified from use with the data sets of this study. Firstly that gaps within the range are not taken account of in the measure. Secondly, the value is often identical among replicate samples, creating variance problems. To avoid these problems, a modification the index calculation was attempted. Calculating richness by dividing the total range of leaf area size into classes was trialled, using number of classes occupied as the measure of richness. However, it was found that with the species density levels and leaf area size distribution of data sets from this study, the number of classes occupied was either too highly correlated with species density, or, did not differentiate among development stages as much as the original form if the index did, depending on experiments with varying class size. Therefore, the original index was adopted.

Functional evenness

The term functional evenness shall be used to refer to the functional regularity index (FRO) (Mouillot et al. 2005) that is based on the Bulla *O* index of species evenness (Bulla 1994). Functional evenness measures the parameter of evenness in the distribution of plant abundance across functional trait space within an assemblage. It is unrelated to both species and functional richness and it has a maximum value of 1, corresponding with maximum functional evenness (Mouillot et al. 2005). Therefore, like Simpson's evenness index, the index value relates to how much an assemblage differs from maximum evenness of the parameter it is based upon. Equations 2.9, 2.10 & 2.11 detail the method for calculating functional evenness:

Equation 2-9 $$FRO = \sum_{i=1}^{S-1} \min(PEW_{i,i+1}, \frac{1}{S-1})$$

where, S is the number of species and $PEW_{i,i+1}$ the percentage of the weighted difference in trait values for species i and i+1 which is calculated as :

Equation 2-10 $$PEW_{i,i+1} = \frac{EW_{i,i+1}}{\sum_{i}^{S-1} EW_{i,i+1}}$$

with:

Equation 2-11 $$EW_{i,i+1} = \frac{|C_{i+1} - C_i|}{(A_{i+1} + A_i)}$$

where $EW_{i,i+1}$ is weighted difference in trait values for species i and i+1. C_i and A_i are trait value and abundance for species I respectively, with species ranked by increasing values of C_i.

Functional difference

The 'functional difference' (*sensu* Walker et al. (1999)) index 'FD_{var}' (Mason et al. 2003) is designed to be orthogonally related to functional evenness (Mason et al. 2003). Its inception stems from the elucidation of ten *a priori* criteria (Mason et al. 2003), deemed to be important for an index of functional diversity. These include that it should reflect the range of character variation present and the abundances of the species with those characters in the species assemblage, but also be unaffected by either the measurement units, or by the species richness as well as other mathematical considerations (Mason et al. 2003).

Functional difference is the degree to which the distribution of biomass in functional space maximises the variation of that trait within a species assemblage and has been identified as an important aspect of functional diversity (Diaz & Cabido 2001). It measures the dispersion of species in character space by calculating the variance (using squared residuals) in the character weighted by the abundance of the species with that character. The index values are able to be compared among assemblages.

Functional difference (Mason et al. 2003) is expected to be the best predictor of ecosystem function among the three trait value based indices (Mason et al. 2005) presented here. The theory behind the link between functional diversity and ecosystem functioning is

related to resource use complementarity (Schmid 2002). The idea being that with greater diversity of a trait, niche complementarity is maximised enabling full use of available resources, which in turn increases the rate of ecosystem functions (Petchey et al. 2004); for example, an increased diversity of leaf architecture captures light more efficiently and increases productivity. Equations 2.12, 2.13 & 2.14 detail the calculation method for obtaining functional difference values:

Equation 2-12 $$w_i = a_i \Big/ \sum_{j=1}^{N} a_j$$

Let a_i= the abundance of species i, out of N species, X= the character value of species i. The relative abundance of species i is w_i

Equation 2-13 $$\overline{\ln x} = \sum_{i=1}^{N} w_i \times \ln x_i$$

The weighted logarithmic mean of the character, $\ln x$

Equation 2-14 $$V = \sum_{i=1}^{N} w_i (\ln x_i - \overline{\ln x})^2$$

The sum of the squared deviations, weighted by the abundances, gives the measure of variation: V

Although Mason et al. (2003) recommend the use of a transformation of 'V' (not shown here) to create the function termed FD_{var} , in this thesis, the functional difference index has been graphed and analysed using values of 'V' (Equation 2.14). This is because considering the range and variance of data values for all study sites, it was found that pattern was more clearly resolved with the index expressed in units of 'V'.

2.2.4.6 Taxonomic distinctness

It is increasingly recognised that biodiversity indices should not solely be based on the number of species present and their relative abundances (Harper & Hawksworth 1994;

Magurran 2003). In response to this recognition, Clarke & Warwick (1998b) have devised the 'taxonomic distinctness' (Δ^*) index that considers only information on the taxonomic distance between species in an assemblage based on the Linnaean taxonomy[19]. The index takes no account of species abundances or richness, conferring the advantage of being independent of sampling effort and species diversity measures (Warwick & Clarke 1995; Magurran 2003). It is sometimes correlated with functional diversity but is considered a separate measure (Petchey & Gaston 2002). Thus, it measures a different aspect of assemblage structure than the other indices. Warwick and Clarke (1995) cite evidence from benthic animal assemblages that the index is sensitive to ecosystem perturbation even when species richness remains unaffected and that values tend to increase with successional progression. An increase in index value corresponds with a greater distribution of species amongst the higher taxa. Therefore, the index is a measure of the evenness of taxa distribution across the hierarchical taxonomic tree (Magurran 2003). Nevertheless, the index is a relative measure with no global validity of values (Warwick & Clarke 1995). However, this does allow the value-independent pattern comparison among seres adopted in this study.

Taxonomic distinctness was calculated using the PRIMER computer programme (Clarke & Gorley 2001b). The input information required is a spreadsheet of the Linnaean classification hierarchy from kingdom down to species level (including phylum, class, order, family and genus) for each sample. From this spreadsheet, the programme constructs a taxonomic tree that is used to produce a relatedness matrix enabling the calculation of the taxonomic distinctness statistic; the 'distance apart' between any pair of species in the sample (Clarke & Warwick 1998). Thus, 'taxonomic distinctness' can be thought of as the average path length between any two randomly chosen different species from within the sample (Clarke & Warwick 1998). The option for non-equal 'step' (i.e. branches in the hierarchical taxonomic tree) lengths (Clarke & Gorley 2001a) was chosen that defines the

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[19] The Linnaean taxonomy is assumed to be an approximation to phylogenetic relatedness (Clarke & Warwick 1998).

weight given to each step as proportional to the percentage of taxon richness accounted for by that step (Clarke & Warwick 1999).

Equation 2-15 Calculation of taxonomic distinctness Δ*.

$$\frac{\left[\sum\sum_{i<j}\omega_{ij}\right]}{\left[\frac{s(s-1)}{2}\right]}$$

Where s is the number of species in the study; and ω_{ij} =the taxonomic path length between species *i* and *j*.

2.2.4.7 DCA axis one

Axis one of DCA is commonly used to represent beta-diversity (*sensu* (Whittaker 1960)), as a measure of species turnover along a vegetation development trajectory (Walker & del Moral 2003). Since DCA units are scaled in terms of percentage floristic change (Jongman et al. 1995), it is an appropriate measure to compare different primary succession seres with. Thus, it is added to the list of univariate indices as a measure of the length of the successional gradient, and, with caution owing to the use of the chronosequence approach[20], rate. However, unless DCA axis one values are converted to absolute change per unit time the index is not a linear measure of species turnover. Instead, as well as species turnover, it incorporates a directional component. For example, if species turnover occurs that is contrary to the general floristic development trajectory, values of DCA axis one can decrease. As long as this aspect is understood, the index is more powerful than if converted to absolute species turnover because species turnover is still easily interpreted and information on the complexity of the compositional trajectory is gained also.

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[20] For inferences to be made about the rate of succession, it must be assumed that; 1) the succession would followed linear trajectories between the stages sampled by the chronosequence method, and, 2) the ages of the stages are accurate. Whilst it is not possible to confirm these assumptions it is felt that general comments about relative rates among stages within sites and among sites are robust.

2.2.5 MULTIVARIATE ANALYSES PART TWO

The following methods of fitting regression models to univariate indices change with age and PCA analysis of species data / all indices values are designed to test thesis question **II** : *Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?*

2.2.5.1 Regression (part two)

The second application of regression analysis (see section 2.2.2.3; regression part one for an explanation of the first application) is to test the relationships between all suitable[21] univariate indices of vegetation development and age as a proxy for vegetation development. These regressions aimed to quantify the following:

- whether the observed pattern of indices change with age best fits a linear or a second order polynomial (i.e. quadratic) model
- the strength of the fit (i.e. the proportion of variance explained)
- the direction and slope of change
- the significance of the relationship between each index and age (i.e. the significance of the slope).

General methods were followed to manipulate variables in order to meet regression assumptions and to screen results (see section 2.2.3.3 for details on weighting, transformation and residual analysis procedures). The methods for the regression procedure to test univariate index response to age is detailed below.

2.2.5.1.1 Linear and second order polynomial regressions

The procedure followed for fitting the two models to each index was to fit the linear model first and subsequently add the polynomial model. The magnitude and

[21] Some indices values and variance rendered them unsuitable for regression analysis; these are specific to each study site and are highlighted within the individual study site chapters.

regularity of the non linear component of each indices' relationship with age varies among indices and sites[22], and, may not be completely described by the models applied. Nonetheless, it was decided that to attempt to apply nonlinear regressions beyond second order polynomials to the data would be spurious (Dr. R. Littlejohn, pers. comm. 2004) because the number of parameters in the equations describing these more complex models would be approaching the number of points in the observed data sets[23] (five or six). Hence, a fit to any of these complex models would be virtually guaranteed and consequently would prove nothing about the pattern of the data.

In the results sections, significance statistics are given for both the slope parameter and the regression itself. The pattern is illustrated by presenting graphs of observed data values with the lines for the fitted model(s) superimposed. Also, to give some idea of the magnitude of the non-fit component of each variable, the percentage variation explained (r^2; otherwise known as the coefficient of determination) is referred to.

In order to test whether the addition of the quadratic term to the previously fitted linear model achieves a significant improvement in the accuracy of the prediction of the indices pattern (i.e. the 'Y' values), an '*F* test' (Zar 1999) is applied where the null hypothesis is that there is no significant difference between the fit of the linear and polynomial models. Thus, rejection of the null hypothesis ($p \leq 0.05$) means that the polynomial model fits the data better than a linear model. The *F* statistic was calculated by dividing the difference between the sum of squares of the linear and polynomial regression by the residual mean square of the polynomial regression. The significance of the *F* statistic was calculated in GenStat by inputting the values for *F* with the degrees of freedom for the numerator being 1, and for the denominator, being equal to the residual DF for the polynomial model.

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[22] Whether this component is of ecological importance or is simply noise is a key topic in the discussion sections of the study site specific chapters.

[23] For example, a third order polynomial model has four functions in the equation describing it, whereas, the observed data has only five or six (mean value per development stage) points, depending on the site.

2.2.5.2 Ordination- Principal Components Analysis (PCA)

2.2.5.2.1 PCA of univariate indices

A PCA analysis was performed on the data for all univariate indices[24] using the CANOCO v4 software package. The same transformations of the indices values as were used for the linear regressions were applied in the PCA analysis. Procedures inherent in the PCA computations deal with any heteroscedasticity of indices among stages (ter Braak & Smilauer 1998). No environmental variables were included in the analysis. Default options were used except for the selection of 'sample separation with post transformation', whereby the sample scores approximate the inter-sample inner products and are derived from a weighted sum of the indices' scores (ter Braak & Smilauer 1998).

The object of the PCA analysis was to reduce the inter-correlated matrix of indices values per sample into the orthogonal components represented by the eigenvectors of the two main axes. The graph of samples drawn from their eigenvectors therefore shows the separation of plots and development stages according to the indices. It is then possible to assess the relative importance and degree of interrelationship between each index in explaining the total variation of all index scores by superimposing the bi-plots onto the PCA graph. Ter Braak (1996) explains that the bi-plots are a slope parameter for the PCA reciprocal regression between sample and indices scores that represents the sample separation due to each index relative to point 0,0 on the graph. It is also possible to compare the separation of samples on the PCA graph with that of the DCA graph to draw conclusions about how much of the total information in the species abundance data-set is lost by reducing it to the chosen group of univariate statistics.

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[24] Soil variables were not used in order to keep consistency in the indices used among the sites because the Godley valley site did not have soil variables measured.

2.2.5.2.2 PCA of species data

A PCA on species data provides a way of summarising the trajectory of recovery of ecological systems (e.g. Myster & Walker 1997; Anand & Desrochers 2004). The basic PCA algorithm involves minimisation of correlations between variables (species) using eigen analysis to produce new components (the axes of the biplot) that are linear combinations of the original variables. In this way, a reciprocal regression holds true between the species scores and the species-derived sample scores (ter Braak & Smilauer 1998). Although PCA is thus essentially a linear technique, with regard to the sum of the interactions between the component variables (the relative position of samples) it is sensitive to non-linearity (Anand & Desrochers 2004). Therefore, it is a suitable tool to study the floristic trajectory of a system through time. Although DCA analysis can be used to assess successional trajectories, PCA is a preferable method for this purpose because it is not prone to bias from rare or very common species like DCA is (ter Braak & Smilauer 1998). Furthermore, it was found with the thesis data sets that the first three axis of the PCA analysis (i.e. those used for a three-dimension trajectory depiction) explained a higher percentage of the species abundance data variation than did the first three axis of the DCA analysis.

Default options were used for all study sites, whereby the scaling of the sample scores (and, therefore, their relative position on the biplot graph) is focused on the inter-species correlations both within each sample and among all samples. In order to present a summarised three-dimensional trajectory, the mean sample score for the first three axes was calculated for each development stage.

3 FOREST REGENERATION AFTER LANDSLIDES AT LAKE THOMSON, NORTHERN FIORDLAND

3.1 OVERVIEW

This chapter shares a general format with Chapters four and five, because in common with those chapters it describes in detail the vegetation development inferred by one chronosequence in such a way that the patterns can be compared among all three chronosequences.

In this chapter, the study site at Lake Thomson, northern Fiordland, South Island, New Zealand, and reasons for its selection are described. The majority of field and analysis methods used for this site are common to the other two chapters describing chronosequences. These methods are described in full in the general methods (Chapter two). Only the aspects of methods that are unique to this site are elucidated in this chapter.

The vascular plant assemblages and environmental characteristics of five development stages, recovering form landslide disturbance and ranging in age from c. 4 to c. 600 years, are analysed. The vegetation development inferred follows a simple trajectory towards a relatively homogenous temperate beech (*Nothofagus*) forest. It is shown that floristic variation within each development stage is less than that among the stages, even between the two stages with the most similar ages. The majority of univariate indices had strong and consistent responses to the vegetation development gradient..

The discussion begins by summarising the evidence to support the chronosequence sampled at this site being of good quality. The remainder of the discussion concentrates on explaining the patterns of change displayed among the set of univariate indices by referring to previous research at this site and at other comparable sites as well as to ecological theory.

3.2 INTRODUCTION

3.2.1 PREVIOUS STUDIES OF SUCCESSION TO FOREST AFTER LANDSLIDE DISTURBANCE

In order to set the findings of this study into the broader context of international scientific research, a literature review was conducted with the scope set as any study of

succession by any method where the disturbance type was a landslide and the vegetation sequence developed towards a forest of any species composition.

In summary, the literature review found that methodologies varied to the extent that it is hard to make detailed comparisons and draw general conclusions. There are few studies that study succession after landslides by means of a chronosequence *sensu stricto*, where due effort was made to reduce variation among stages in factors other than time and that development stages sampled were distributed over the entire vegetation development gradient present. Most studies either inferred successional patterns by means of sampling numerous widely distributed landslides of various unknown ages, or, recorded changes by direct observation. However, direct observations were conducted on a small number of landslides only as well as being over a short time period relative to the length of time required for an entire vegetation development gradient to proceed.

Studies were found to be largely concentrated within a few areas of the world. Much effort has taken place in the Caribbean, particularly Puerto Rico (e.g. Guariguata 1990; Walker & Neris 1993; Zarin & Johnson 1995; Walker et al. 1996; Myster et al. 1997; Myster & Walker 1997; Frizano et al. 2002), the United States (e.g. Hull & Scott 1982; Miles & Swanson 1986; Francescato et al. 2001; Pabst & Spies 2001; Restrepo et al. 2003) and New Zealand (e.g. Mark et al. 1964; Mark et al. 1989; Blaschke et al. 1992; Smale et al. 1997), with a couple of studies in South America (e.g. Veblen & Ashton 1978; Wilcke et al. 2003).

In general, methods did not involve accurate measurement of the time since disturbance. Neither were they able to determine the intensity of the disturbance, in particular with respect to the level of ecological legacy that would have remained after the disturbance event. Nonetheless, irrespective of time scale, most studies reported that vegetation development, at least within the same zone of the landslide (i.e. slip face versus debris pile) follows a reasonably predictable single pathway tending towards pre-disturbance condition (e.g. Mark et al. 1964; Nakamura 1984; Guariguata 1990; Reddy & Singh 1993; Smale et al. 1997; Francescato et al. 2001; Pabst & Spies 2001), albeit with spatial variation of the precise composition of species assemblage.

Where time since disturbance was measured, rates of succession varied considerably between ecosystem type, development stage replicate samples and type of indicator used. For example, Dalling (1994) showed that biomass of colonising vegetation in the Blue Mountains of Jamaica took c. 500 years to approach that of pre-disturbance condition, whilst basal area, plant biomass and soil nutrients in the Luquillo mountains of

Puerto Rico only took c. 55 yrs (Zarin & Johnson 1995). After 45 years, two apparently identical adjacent landslides in the White Mountains of New Hampshire (those first studied by Flaccus (1959)) had plant covers of c. 80 % and c. 55 % (Francescato et al. 2001). Smale et al. (1997), in a study of 24 landslides at seven sites within the East Cape region of North Island, New Zealand found that vegetation height, composition and soil depth changed at remarkably even rates, whereas stem density did not. Reddy and Singh (1993) compared the trajectories of two distinct communities that occur at different altitudes within the same region of the central Himalayan mountains. They found that soil organic carbon and herb layer cover increased by a factor of three every 25 years in one community, yet increased by a factor of five in the same time span for the other. In contrast, species richness showed a similar rate of increase between the two communities. Interestingly, rates of change aside, all the indices Reddy & Singh (1993) measured showed the same pattern among sites.

The indicators used to track vegetation development among previous studies are similar and the total variety is surprisingly small. Plant biomass (either estimated or directly measured) (e.g. Reddy & Singh 1993; Dalling 1994; Restrepo et al. 2003), soil nutrient concentrations (e.g. Guariguata 1990; Reddy & Singh 1993; Zarin & Johnson 1995; Wilcke et al. 2003), and cover abundance of specific growth forms or taxa are the most common (e.g. Guariguata 1990; Francescato et al. 2001). Other indicators used are multivariate measures of floristics (e.g. Myster & Walker 1997; Pabst & Spies 2001), structural complexity (e.g. Myster et al. 1997), species richness (e.g. Nakamura 1984; Reddy & Singh 1993) and coefficients of floristic similarity (e.g. Mark et al. 1989).

With regard to landslides in the same forest type as the study site of this chapter, prior to the two research visits by Alan Mark and colleagues in 1962 and 1986 made to the study site itself (Mark et al. 1964; Mark et al. 1989), successional vegetation on landslides in Fiordland had only briefly been described. In particular, Poole (1951) noted the importance of landslide succession in determining forest composition in the valley-side forests of the region around Lake Thomson, observing that a forest dominated by silver beech and southern rata gradually returns after disturbance. The first study by Mark et al. (1964) assessed the structure and composition of the chronosequence by sampling at 25 points within a belt between 330 and 360 m a.s.l. in four development stages. The second study (Mark et al. 1989) re-sampled the same areas using the same methodology, with the partial aim of assessing the accuracy of the succession previously inferred by means of a

chronosequence against direct observation of the changes that had occurred in the intervening 24 years.

The present study uses a different methodology to those used by Mark et al. (1964) and Mark et al. (1989) because it has different objectives. Thus, results among the three studies are not directly comparable. This study is intended to provide a more precise analysis of the relative species abundances within the vascular plant assemblages occurring along the vegetation development gradient. Therefore, this study is designed to be able to quantify the patterns of vegetation development by additional means whilst also measuring the spatial variability within each development stage over a larger scale.

3.2.2 FACTORS OTHER THAN TIME AFFECTING VEGETATION DEVELOPMENT AFTER LANDSLIDE DISTURBANCE

Studies of landslides are still uncommon and mechanisms of succession during landslide revegetation are poorly understood, moreover, experimental designs have rarely enabled the testing of landslide successional trajectory predictability and what variation is dependent on (Walker et al. 1996). One attempt at testing trajectory predictability studied the first five years of landslide development among 16 landslides in the Luquillo experimental montane forest, Puerto Rico concluded there was no predictable pattern (Myster & Walker 1997). The authors cited the stochastic nature of plant dispersal and priority effects of initial colonisers as the most likely causes of multiple development trajectories. However, the study encompassed too short a time span to assess if trajectories would have continued in parallel, diverged or converged. Another study in Luquillo forest, Puerto Rico tested the predictive value of landscape characteristics for the structural diversity of vegetation growing on landslide, finding that the two factors of importance apart from age were initial substrate type and aspect (Myster et al. 1997). This finding emphasises the importance of reducing environmental variation among chronosequence sites.

In a review of landslide succession research in the Caribbean, Walker et al. (1996) suggested that factors influencing the rate and trajectory of plant succession included elevation, size, surrounding vegetation (light availability and seed rain), and, initial substrate conditions, particularly the amount and type of remnant soil (availability of propagules and nutrients). Studies from elsewhere highlight landslide width, slope (Francescato et al. 2001) and grazing activity (Smale et al. 1997) as also being significant determinants of floristics. No study in the literature, except perhaps for those conducted

previously at the Lake Thomson site, was found to have a sampling design that either was able to control for all variables other than time, or, on account of the prevailing conditions was able to keep variation of all factors other than time down to a negligible level. Thus, the conclusions of all these studies with respect to vegetation development trajectory analysis are compromised, to a greater or lesser extent, by multiple un-measured variables. Nonetheless, there is a growing body of research that has increased our ability to characterise the patterns of forest succession after landslide disturbance.

At the Lake Thomson study site factors other than time and measured environmental variables that I perceived to be possibly significant determinants of floristic variation centre around conditions that prevailed during the establishment phase of each landslide. For example; soil legacy, seed rain, climate, grazing and water availability.

This Chapter seeks to address the first two thesis questions in the context of the data from the Lake Thomson chronosequence:

I. *How do floristics vary with age and does the main floristic gradient correlate more closely with age than any other environmental variable ?*

II. *Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?*

3.3 METHODS

The methods section follows a logical order from site selection and description to field data collection methods, then finally on to the analysis tools used to examine the floristics information recorded. The majority of the field and analysis methods are common to Chapters four and five that detail the vegetation developments at the other two sites. Common methods are described in full in the general methods, Chapter two. Only the aspects of the methods that were unique to the Lake Thomson site are fully explained in this chapter.

3.3.1 STUDY SITE

3.3.1.1 Site selection rationale

The study site was chosen because a literature search and consultation of experienced New Zealand ecologists (Prof. A.F. Mark, Assoc. Prof. D. A. Norton, Dr. L Burrows pers. comms. Oct 2002), found it to be the only known example in New Zealand of vegetation development after landslide disturbance that approached a chronosequence

sensu stricto. Also, the existence of baseline data published by Mark et al. (1964) and Mark et al. (1989) was attractive since this was the first study site.

The landslides are directly adjacent to one another, so there is negligible variation in environmental characteristics (geology, aspect, slope, soil type, climate etc.) among them. Indeed, Mark et al. (1964, p 62), concluded that "time is probably the most important differentiating factor in the vegetation of the slip faces". Furthermore, initial conditions are likely to have been similar among the landslides based on the assumption that the five development stages would have had a similarly low level of ecological legacy left behind after their respective landslide disturbance events. The evidence for this assumption is that the faces of other recent landslides in the vicinity of the study site, that are on the same rock type and have similar slope and aspect, all had minimal amounts of debris left on the bedrock.

3.3.1.2 Study site description

Figure 3.1 shows the location of the study site in a remote part of northern Fiordland. The site is above the southern edge of Lake Thomson, and well within the boundary of Fiordland National Park. Its western edge is approximately 400 m east of the outflow of Lake Wade (coordinates: 167° 55' E, 45 ° 10' S). The study site consists of four development stages on recent landslides that run parallel to each other plus an area of directly adjacent mature forest. The five stages all extend from c. 700 m a.s.l. (approximately the poorly defined tree line) down to lake level (280 m a.s.l.). These stages all have obviously distinct plant assemblages and together form a remarkable chronosequence that occurs within a 200 m wide strip of mountain-side with an almost uniform north-northeast aspect and steep slope.

Successive Pleistocene and Holocene ice advances have created the landscape of the northern Fiordland region (McKellar 1982). Typical features are the deeply eroded, steep-sided valleys, lake basins and sharp mountain peaks (up to 1800 m) (McKellar 1982). Because of their steep, extremely smooth bedrock the valley sides are prone to landslides that can be triggered by intense rainfall, earthquakes or snow avalanches (Mark et al. 1964), and when landslides occur very little soil is left behind. Thus, the ecosystem is adapted to regular disturbances. Indeed, the regeneration of *Nothofagus* spp. (the dominant canopy taxa of the study site) in New Zealand generally follows the stand replacement process whereby even-aged stands develop in large gaps after disturbances (Stewart 1986).

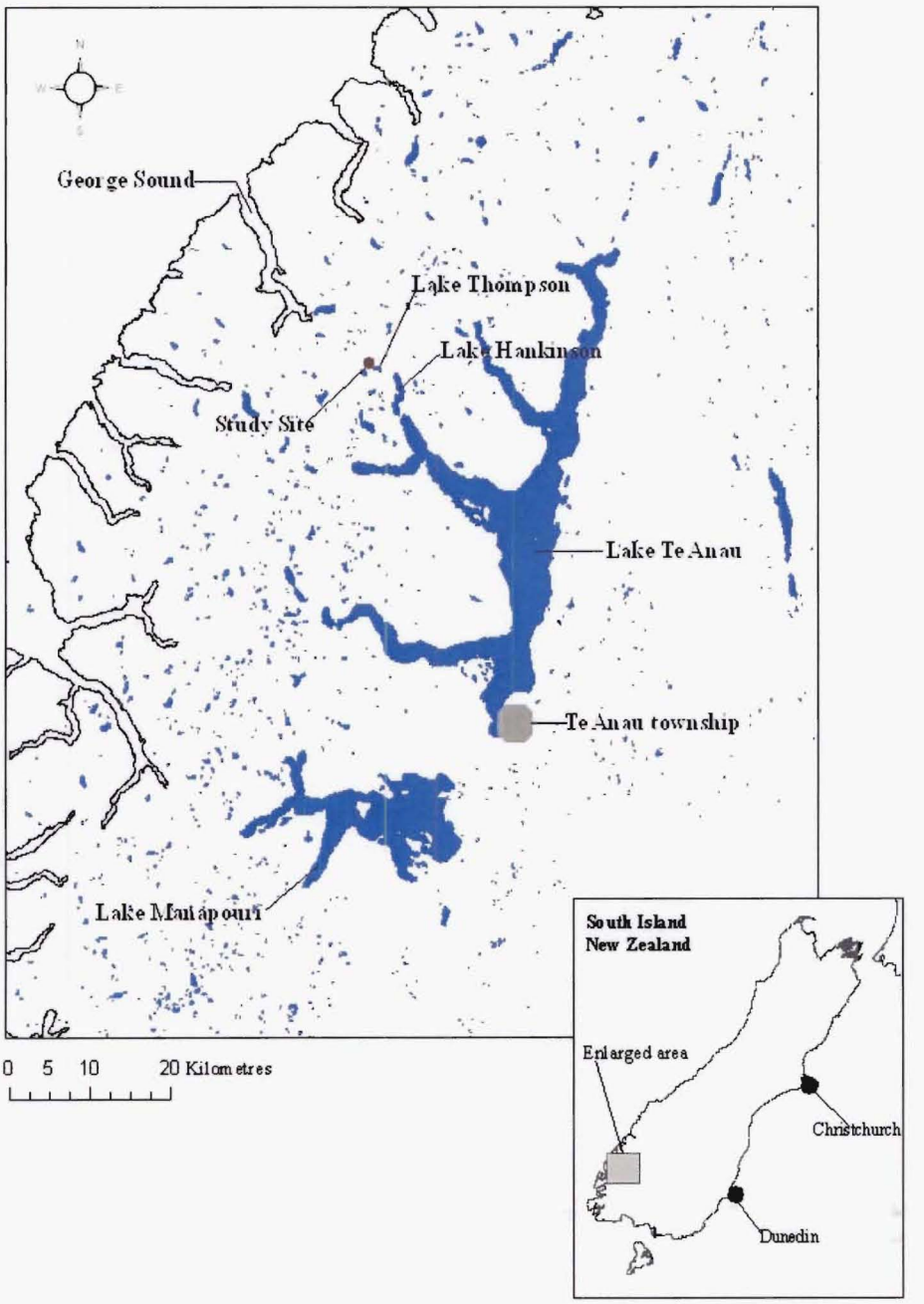

Figure 3.1 Map showing the location of the Lake Thompson study site within the South Island, New Zealand

The rock type that exists in the study site is classified as plagioclase-biotite-hornblende gneiss (Wright & Carter 1965). Gneiss is a high grade metamorphic rock of grey-pink colour, coarse texture and distinct banding which tends to produce low fertility acidic sandy soils (Wright & Carter 1965). Soil at the study site develops to form a peaty loam layer over a sandy silt (Mark et al. 1964). There are no climate recording stations in the area, however the climate type of the region is wet temperate. Local rainfall estimates derived from Isohyet maps (New Zealand Meterological Service 1973) are 6200 mm per annum.

The vegetation type that occurs on all undisturbed areas in the vicinity of the study site below around 500 m a.s.l. is tall forest dominated by *Nothofagus* spp. The community type corresponds with the 'mountain beech-silver beech-kamahi' type that previous surveys of the region found to occupy most of the lower slopes of northern Fiordland east of the main divide (Wardle et al. 1971). Several large introduced mammals are present in the study area. Populations of Wapiti (*Cervus elaphus nelsoni*) and Red deer (*Cervus elaphus scotius*) peaked in the middle of the 20th Century, causing severe browsing of the understory (Stewart 1986), however numbers are now comparatively low as a result of wild animal control (Dr. L. Burrows pers. comm.) and some recovery of the vegetation has occurred (Wardle 1984).

Four of the development stages occur on landslides recent enough to still exhibit obvious evidence of the extent of the disturbance event, displayed by discontinuities in vegetation type and stature. They all consist of two parts: a slip face, from which almost all of the soil and vegetation is assumed to have been removed from, and below this, a lower debris-fan comprised of the accumulated slip material. The fifth development stage is assumed to have been subject to similar disturbance events in the past and now supports mature forest. The different landslides vary in average width, the narrowest being only c. 30 m and the widest c. 70 m. The width of each landslide varies very little with altitude.

In the view shown in Figure 3.2 overleaf, the chronological order of the development stages from right to left can be seen, with one being the youngest and five being the oldest. The development stages are referred to by these numbers hereafter. In this study, development stages two to five are the same as 'stands' one to four that were sampled by Mark et al. (1964), and re-sampled by Mark et al. (1989). Development stage one has regenerated from a further landslide event that occurred in c. 1998, after the last study by Mark and colleagues.

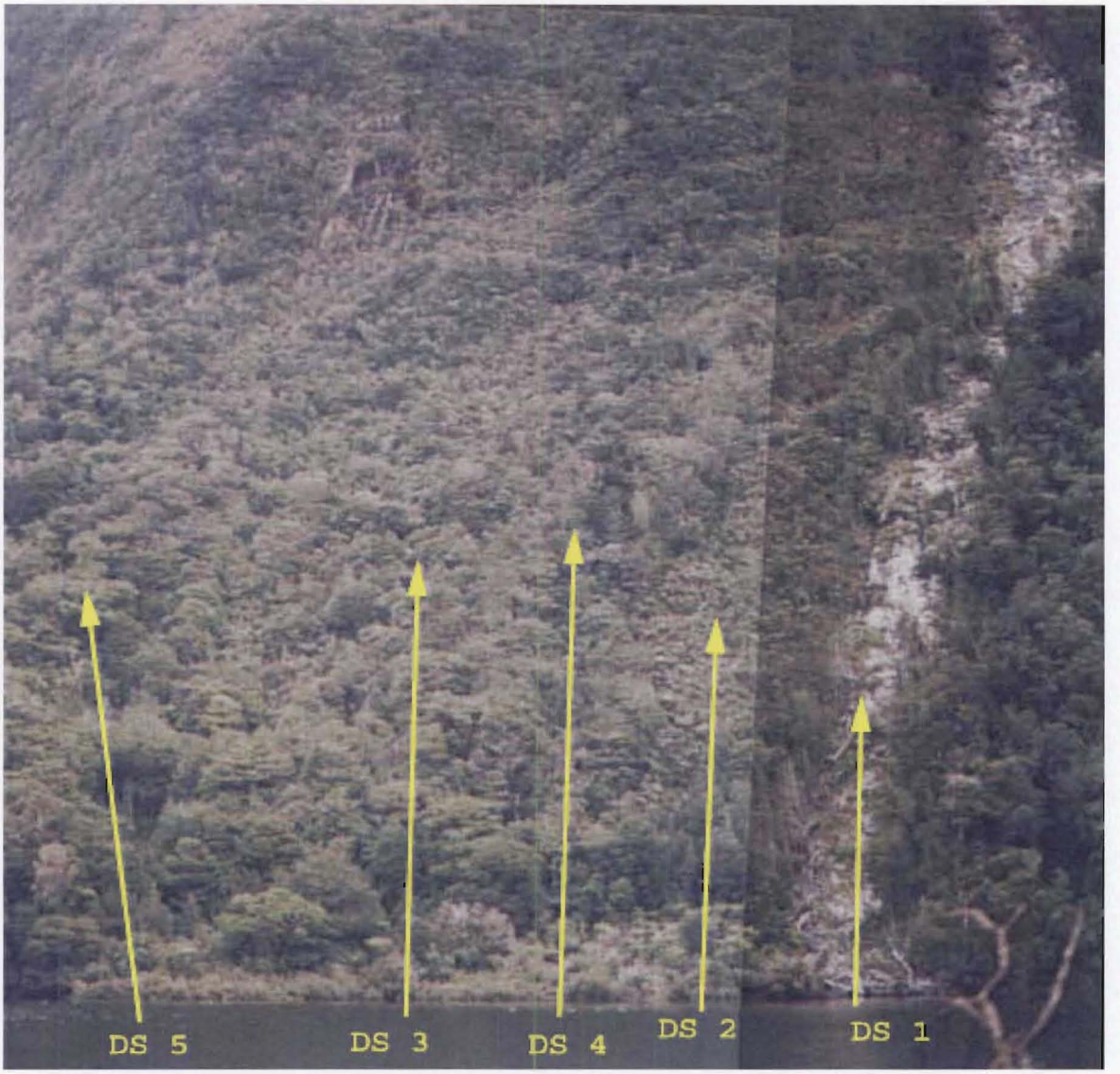

Figure 3.2 View of the study site from the opposite side of Lake Thomson showing the different development stages, four of which are recovering from relatively recent landslides and the other being mature forest. The distinct vegetation of the debris fans at the base of the landslides can be clearly seen.

3.3.2 FIELD METHODS

This section includes a description of the sampling design used, how development stages were aged and details of sampling techniques for the environmental variables, soil sampling and plant abundance estimation.

3.3.2.1 Field-work

Two trips, each over a fortnight in duration, were made in December 2002 and April 2003, both with field assistants (see acknowledgements).

3.3.2.2 Sampling design

3.3.2.2.1 Stratified random method

Figure 3.3 gives a schematic representation of the distribution of sample plots. Only the upper face portion of the landslides were sampled. The fans were unsuitable for sampling because, as Mark et al. (1989) also observed, not only is the vegetation different from the landslide faces above but, moreover, the plant assemblages corresponding to the different landslide events are not easily discernible. The lowest plots were located at 300 m a.s.l. (c. 20 m above lake level), well above the top of the landslide debris fans.

Ten plots were sampled per development stage (except for DS 3 which had only nine samples owing to bluffs) to characterise as much of the floristic variation within each development stage as possible. One plot of this study per stage was placed inside the permanent plots instigated by Mark et al. in 1986 for the development stages that existed (two to five) at the time of their work. With respect to the chronosequence concept, these 10 plots established on each stage are, *sensu stricto*, pseudoreplicates.

Of the total of 49 plots sampled, all except three were located in an altitudinal range from 300 m to 425 m[1]. In case the 125 m altitude range was enough to affect floristics, the sampling was stratified to ensure an even altitudinal distribution of plots among development stages. This was achieved by dividing the altitude range into five 25 m bands and placing two plots for every stage in each. Nonetheless, previous research very close to the study site indicates that altitude variation within this range should not be an important determinant factor for the structure or composition of species assemblages (Scott et al. 1964).

Within each altitudinal band of each landslide, the exact position of the plots was randomly located using binomial coordinates generated by random number sheets.

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[1] In development stage one, the excessive steepness at various points pushed the upper three plots to 435, 505 & 515 m respectively)

3.3.2.2.2 Plot location criteria

Random coordinates were followed to locate a point that, providing it fitted within the following plot location criteria, was determined as the upper-western corner of each plot:

- Slope was not outside a range of 30 – 45 degrees.
- At least 10 m separated the closest point of the nearest plot.
- Physiography being a roughly linear face
- Minimal evidence of grazing

The boundary of each plot was defined by travelling first perpendicular and then parallel to the slope using measuring tapes to avoid subjectivity of placement.

3.3.2.2.3 Sampling effort

A plot size of 10 by 10 m was decided upon by drawing upon the collective experience of previous forest surveys conducted in 'beech-hardwood' ecosystems of the South Island, New Zealand, similar to that of the study site. For the species assemblages known to exist within the vegetation development sequence typical of the study area (Mark et al. 1964; Wardle et al. 1971), a 10 by 10 m plot was thought to be a sufficiently large unit with which to sample, taking into account the species diversity and size of the largest individuals (D. Norton pers. comm. September 2002).

A sample size of 10 was considered to be adequate to sample the species diversity present within the most diverse development stage. This judgement was based upon the high number of rare species recorded by Mark et. al. (1964) from the most diverse assemblage they sampled using the point centred quarter method, which in total would have surveyed a similar area to 10 samples of the type used in this study.

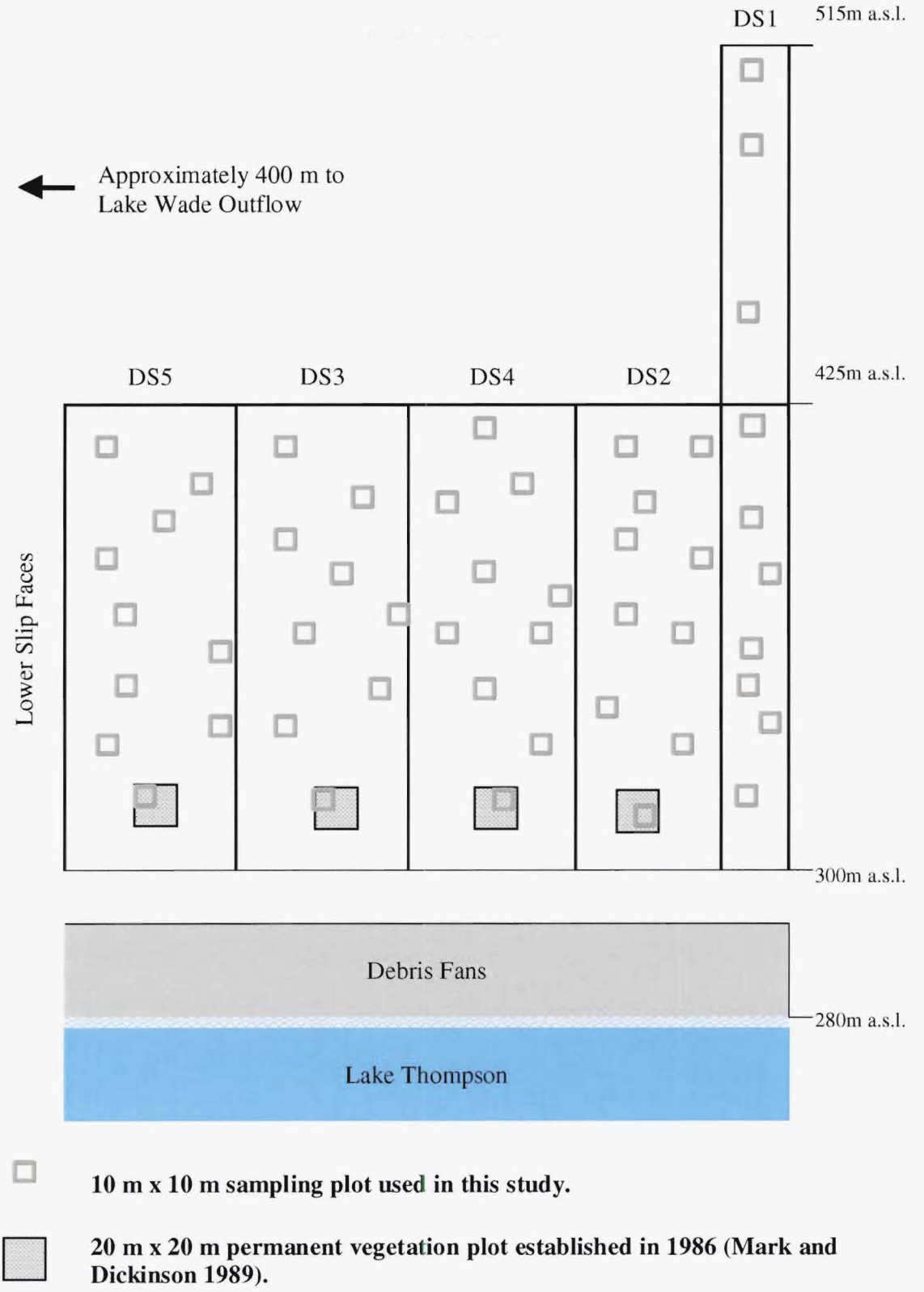

Figure 3.3 Schematic diagram of the Lake Thomson study site sample distribution.

Species accumulation curves constructed from the entire data set[2] illustrated in Figure 3.4 show an early inflexion and a distinct flattening towards their ends. These results provide evidence that further sampling from each development stage would have picked up progressively fewer novel and rare species.

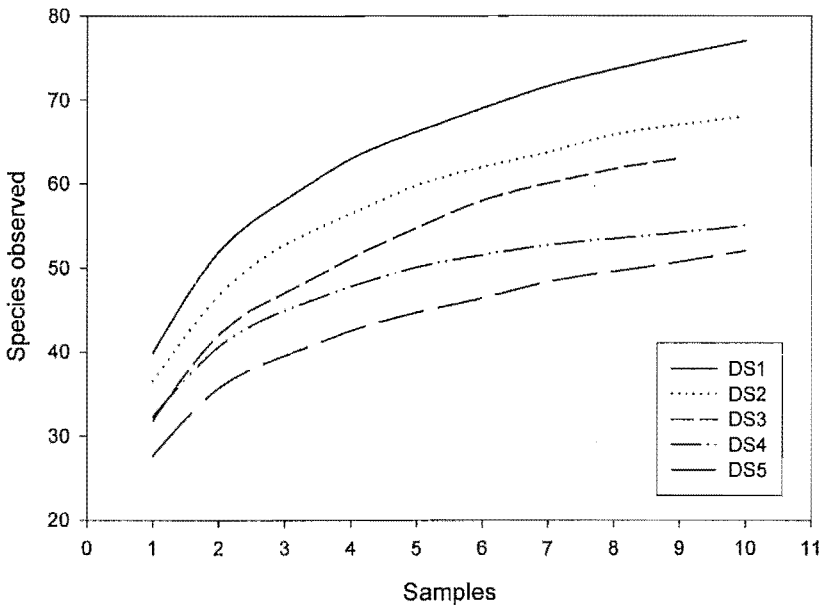

Figure 3-4 Smoothed species accumulation curves for the five development stages

Estimates of species richness (S_{max}) for each development stage, using standard thesis methods, provide a benchmark against which quantitative evidence of adequate sampling effort is derived. Table 3.1 shows the proportion of S_{max} cumulatively observed (S_{obs}) to be high for each development stage, equating to adequate sampling effort. Furthermore, the standard error of the mean among all development stages of the 'proportion of S_{max} observed' figure (85.9 % ±1.11) provides evidence of an even effort among stages. Figure 3.5 gives a graphic illustration of these results.

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[2] See general methods, Chapter two for a detailed description of methods for constructing species area accumulation curves

Development stage	S_{obs}	S_{max}.	S_{max}. SD	proportion of S_{max} observed (%)
1	77	91	2.75	84.2
2	68	78	3.66	87.3
3	63	75	3.56	84.5
4	55	61	3.56	89.7
5	52	62	2.83	84.0

Table 3-1 Results per development stage of: 'S_{obs}' observed species area accumulation data, 'S_{max}' estimate of species richness (Jacknife 1 estimator of maximum theoretical assemblage species richness observable assuming exhaustive sampling), 'S_{max} SD' standard deviation of the species richness estimate and the proportion of S_{max} cumulatively observed.

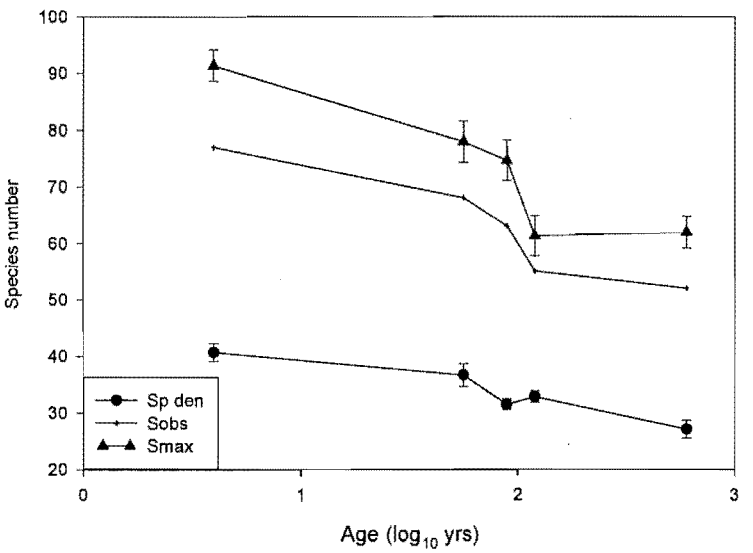

Figure 3-5 Three measures of species diversity per development stage for comparison. Sp den= mean species density (species observed per replicate sample) with standard error bars, S_{obs}= observed species richness from accumulated replicates' sample data, and S_{max}= mean estimated theoretical maximum species richness (assuming exhaustive sampling) and standard deviation bars.

Figure 3.5 illustrates even sampling effort among stages because the curves for S_{max}, S_{obs} and species density are almost parallel. This means that comparison among stages of indices related to aspects of species diversity (see univariate indices calculation methods, Chapter two) are robust.

3.3.2.3 Development stage ageing

Ages for the middle three stages (DS 2, DS 3, and DS 5) were calculated by Mark et al. (1964) using *Leptospermum scoparium* (manuka) growth rings, using the assumption that rings were produced annually. Their methodology of sampling the oldest *L. scoparium* individuals found in each of the landslide slip faces, and allowing two years for growth to height of sectioning (20 cm) was repeated in this study to calculate the age of the youngest stage (DS 1).

The historic disturbance regime of the mature forest development stage (DS 5) is unknown. However, since the stand of mature canopy beech trees present is relatively even-aged, it is assumed to have developed from a catastrophic disturbance event such as a landslide. The fact that *Nothofagus menziesii* (silver beech) seedlings are able to establish very soon after disturbance (Stewart 1986, and personal observations) means that the age of DS 5 would be very similar to the age of the oldest trees present in it, provided the assumption of catastrophic disturbance is correct. The age of the largest silver beech tree present was estimated from Diameter at Breast Height (DBH) measurements taken by A. F. Mark in 1962. Estimates were based on existing silver beech age-diameter models (Wardle 1970; Herbert 1973) from the Fiordland district.

3.3.2.4 Environmental variable measurement

Environmental variables recorded in the field using standard thesis methods were slope, altitude and soft sediment depth. Aspect was measured using a surveying compass.

3.3.2.5 Soil sampling

Soil sampling for measurements of pH and organic carbon was conducted using the standard thesis methods. Samples inside air-tight bags were kept as cool as possible by suspending them in running stream water for up to 10 days whilst still in the field, before being frozen for longer term storage until analysis.

3.3.2.6 Cover abundance estimation

Cover abundance was estimated using standard thesis methods. Up to six tiers were identified in the plant assemblages present in this study site. These tiers were named by the following descriptors: ground, shrub, small tree, sub-canopy, canopy and epiphyte. In younger development stages multiple tiers were often discounted as absent, for example, in DS 2 where vegetation stature was low but a definite manuka canopy had formed, the sub-canopy and small tree layer were considered absent. In addition, ground cover abundance

data was collected to the nearest five percent for five categories of cover type; vascular plants, non-vascular plants, leaf litter, exposed soil and exposed rock.

3.3.2.7 Plant species identification

Plant species identification follows standard thesis methods.

3.3.3 ANALYSIS TOOLS

The analysis tools employed for the Thomson data set are mostly the same as those used for the other two study sites. Briefly, they include exploratory data analysis, vegetation description, a suite of multivariate analyses and the calculation of a range of univariate indices. Multivariate analyses performed on the data include two types of ordination; correspondence analysis and principal components analysis, an analysis of similarities and various regressions using different models and methods.

3.3.3.1 Exploratory data analysis (EDA)

A thorough EDA was conducted on the raw data for species and environmental variables as well as the univariate indices using the standard thesis methods. The variation in aspect was considered low enough for it to be treated as being on a linear scale rather than the circular scale it is measured on. Prior to all multivariate analyses, all variables were transformed which displayed a functional relationship between value and variance. Transformations adopted were; the natural log function for organic carbon and cube root for importance score. Cube root was chosen for importance score because it is measured in units of volume.

3.3.3.2 Vegetation description

The average plant assemblage present in each development stage is characterised by three means using standard thesis methods: a compositional summary table is calculated, a specific name is derived and the key structural features are described.

3.3.3.3 Ordination – DCA & DCCA

The ordination methods of Detrended Correspondence Analysis (DCA) and Detrended Canonical Correspondence Analysis (DCCA) were used in tandem to describe the pattern of floristic variation among all the samples, and to assess relationships with environmental variables using the standard thesis methods and options therein.

Environmental variables included in the analyses were altitude, slope angle, aspect, pH, organic carbon, soft sediment depth and age. Variance Inflation Factors (VIFs) printed

in the log file were checked for evidence of excessive multicolinearity of environmental variables and none were high enough to warrant exclusion of any variable from the DCCA analysis. The most multicolinear variables were soft sediment depth and age; the weighted correlation matrix in the log file showed them to be well correlated (r=0.63) but evidently this was not high enough to bias the computations.

3.3.3.4 ANOSIM

An ANOSIM was conducted on the species abundance data to test for significance of difference in floristics among development stages using the PRIMER package, using standard thesis methods.

3.3.3.5 Regression part one

For the Thomson data, regression analysis is used to investigate two questions:

1. Do selected environmental variables explain a significant amount of either of the main floristic gradients?
2. Are indices dependent on age, how strong is their response and is their response trajectory best described by a linear or a polynomial model?

In accordance with the structure of the general methods Chapter, the methods and results pertaining to these questions are split between two parts of regression analysis. The first question is covered in part one and second question in part two. A full explanation of all methods can be found in Chapter two.

The primary step for all regressions was to check if transformations were required owing to a functional relationship between a variables' value and variance being the case. Importance score was transformed using the cube root and organic carbon using the natural log, all other indices were used in their untransformed state. The second step was to ascertain if levels of heterogeneity of variance among stages for each variable (including those transformed) were high enough to require weighting using Bartlett's test. The results for the Bartlett's test are presented in Table 3.2. Those variables requiring weighting had individual weights automatically assigned to each stage for the regression analysis.

	Bartlett's test results		
Univariate index	χ^2	**'p' value** (d.f. =4)	**Requires weighting?**
pH	18.36	<0.001	Y
Organic carbon (%) *	5.25	0.263	N
Sample importance score (m^3 cover)*	6.09	0.193	N
Species density (n per 100 m^2)	6.71	0.152	N
Simpson's diversity (-lnD)	5.81	0.214	N
Simpson's evenness ($E_{1/D}$)	6.32	0.177	N
Distance from lognormal (ΔL)	17.29	0.002	N
Shannon's growth form diversity (H')	8.56	0.073	N
Functional evenness (Fro)	6.86	0.143	N
Functional difference (V)	19.82	<0.001	Y
Taxonomic distinctness (Δ*)	2.42	0.658	N
DCA axis one (S.D.)	11.61	0.021	N
Environmental variable			
Soft sediment depth	7.25	0.092	N

Table 3-2 Results of Bartlett's test for homogeneity of variance for all indices and environmental variables subjected to regression. '*' denotes that a transformed version of the variable was used in the test. The critical value for rejection of homogeneity of variance was $p \leq 0.01$.

3.3.3.5.1 Testing the influence of selected environmental variables on floristic variation

All environmental variables measured at the Lake Thomson site were included in both the DCA and DCCA ordination analyses and only one apart from age (SSD) was significantly correlated with either of the main DCA axes. Therefore, only SSD was selected for stepwise regression analysis. Standard thesis methods were followed exactly for stepwise regressions.

3.3.3.6 Calculation of univariate indices of vegetation development

All univariate indices were calculated using the standard thesis methods.

3.3.3.7 Regression part two

The question that the methods detailed in this section sought to answer was: Are indices dependent on age, how strong is their response and is their response trajectory best described by a linear or a polynomial model?

Functional richness was unsuitable for regression analysis because of extreme heterogeneity of variance among development stages; this could not be remedied using the

standard weighting option because some stages had a variance of 0. All remaining indices were subjected to a test regression analysis using weighting options to check the residuals. Simpson's diversity had one high leverage value taken out. No other indices had any values with either a high leverage, or, large standardised residuals. Finally, the regressions were run from which results were taken. Each individual index was sequentially fitted to age with linear and polynomial models. Results of these regressions were used to test which model had the significantly better fit.

3.3.3.8 Ordination - PCA

Principal components analyses (PCAs) were performed on the species and indices data, using the standard thesis methods, except that the index functional richness was omitted from the indices analysis after an inclusive trial proved it to unduly affect the sample values. This is unsurprising since functional richness was rejected by GenStat as unsuitable for regression and PCA analysis is based on multiple regression calculations.

3.4 RESULTS

The format of the results section follows the same order as has been used in both the general methods Chapter, and in the methods section of this Chapter. Briefly, field data summaries precede the results of analysis procedures.

3.4.1 FIELD DATA

Results from field data include ages for each development stage and a summary of the environmental variable data.

3.4.1.1 Surface ages

Estimated age for each stage is presented in Table 3.3. Development stage one was estimated to be four years old, from growth increments of manuka (*Leptospermum scoparium*) stems. Development stages two, three and four ages follow those published by Mark et. al. (1964), with an allowance made for the time elapsed since then. Development stage five has an estimated minimum age of c. 600 years from DBH measurement of the oldest extant silver beech (*Nothofagus menziesii*).

Development stage	Estimated age
1	4
2	56
3	90
4	119
5	600

Table 3-3 Estimates of the age (time elapsed since landslide event) of each development stage sampled.

3.4.1.2 Environmental variables

Figure 3.6 (overleaf) represents the summary statistics of the measured environmental variables. Results for soil chemical properties are presented in the univariate indices section because they are treated as indicators of vegetation development.

Older landslides' slopes are less than those of younger landslides and the variation within stages is low. The trend among stages is perceptible on the ground; from a distance, the slope of the whole mountainside decreases slightly towards the older stages as the break in the valley wall provided by the Lake Wade outflow is approached. Within each stage, the variation in slope is due to undulations in the bedrock that are on a larger scale than plot dimensions. Mean altitude is virtually even among development stages two to five. These stages also share a roughly even variation in altitude within them. Stage one clearly has a higher mean and range of altitude than the other stages. Soft sediment depth (SSD) increases steadily with age. This is to be expected since soil development will act to increase the depth of the soil profile with time. SSD is not very variable within each development stage. If soil development rates are assumed to be even among even aged samples, low levels of variation within stages indicates that little soil was left behind after the disturbance events and that deposition of inorganic sediment or soil erosion by water is minimal. Aspect is very similar across the whole study site, with the range of the stage means being 20 – 30 degrees.

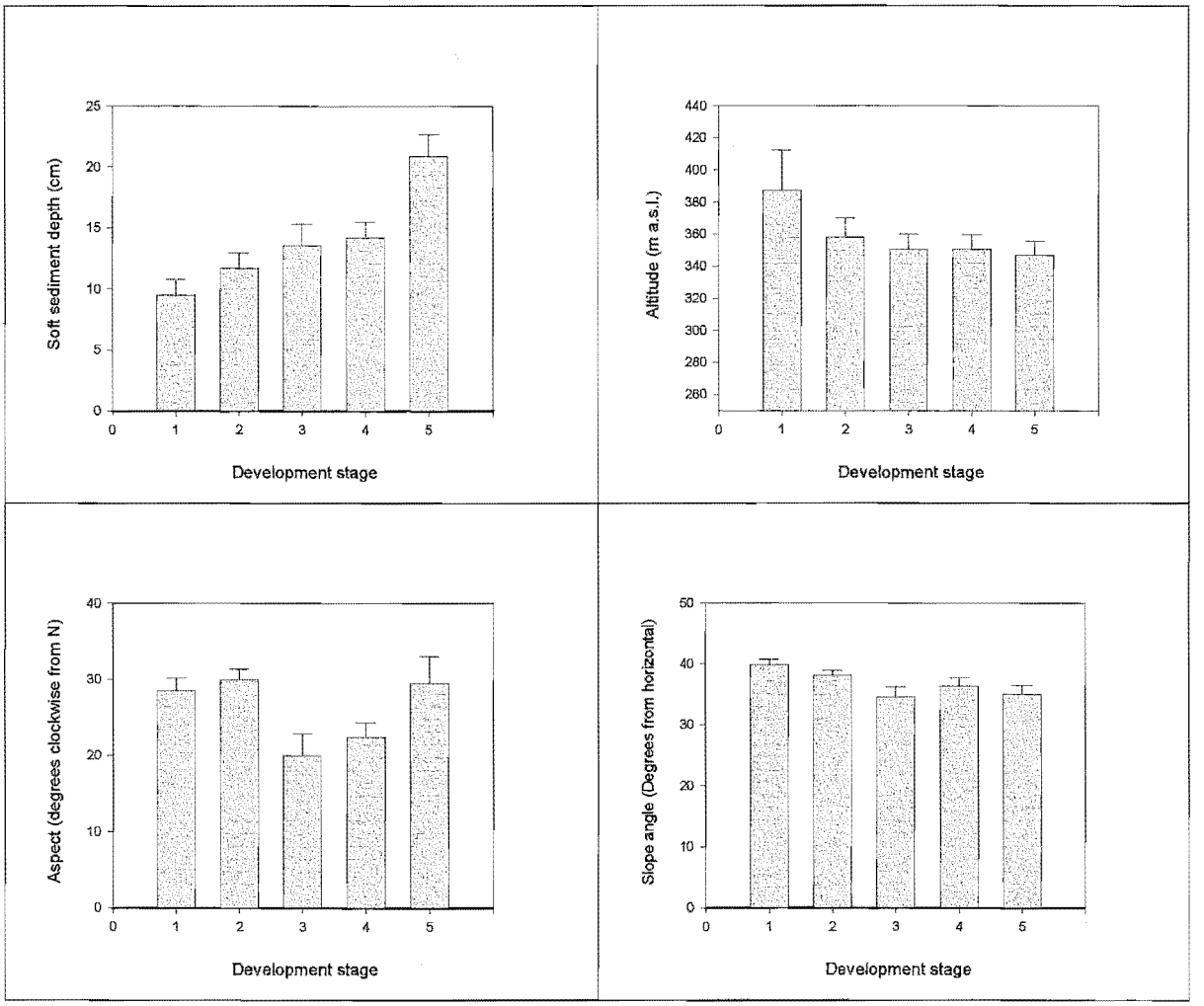

Figure 3-6 Graphs presenting the mean per development stage and standard error of the mean for each environmental variable measured.

3.4.2 RESULTS OF ANALYSES

All results are based on the analysis of vascular plant species data obtained for each sample, some analyses also combine measurements of environmental characteristics. Table 2.1 (page 25) summarises data inputs for each analysis.

3.4.2.1 Development stage vegetation descriptions

The composition of each stage is summarised in Table 3.4.

Species	Development stage 1	2	3	4	5
Blechnum novae-zelandiae	**9.2**	**65.7**	**44.7**	**34.0**	8.6
Nertera ciliata	**8.5**				
Carex solandri	3.6				
Gunnera monoica	2.0				
Phormium cookianum	1.5				
Hebe salicifolia	1.4				
Leptospermum scoparium		**36.4**	8.6	1.3	
Weinmannia racemosa		**24.2**	**28.4**	**47.9**	**63.6**
Nothofagus solandri var. *cliffortioides*		16.6	12.2	**47.3**	**23.9**
Blechnum procerum		6.8	7.6	10.0	5.6
Metrosideros umbellate		6.5	**26.6**	**38.6**	8.6
Nothofagus menziesii		4.1	12.7	9.7	**28.5**
Pseudopanax colensoi		3.4	2.8	1.6	
Coprosma foetidissima		3.2	6.7	13.8	3.5
Raukaua simplex		2.5	4.8	4.3	1.4
Cyathodes juniperina		2.0	2.0		
Coprosma lucida		1.9			
Coriaria arborea		1.8			
Gaultheria rupestris		1.5			
Coprosma colensoi		1.5	2.9	3.1	2.3
Gahnia procera		1.4	2.1		
Lycopodium scariosum		1.4	1.0		
Griselinia littoralis		1.3	3.4	1.7	1.5
Myrsine divaricata			6.0	2.5	1.0
Lycopodium volubile			3.4		
Dracophyllum longifolium			1.8		
Carpodetus serratus			1.7	1.2	
Podocarpus hallii			1.6	1.0	4.2
Pseudowintera colorata			1.2		1.7
Pseudopanax crassifolius				2.0	2.3
Astelia nervosa				2.0	
Phyllocladus alpinus				1.2	
Blechnum discolour					**38.1**
Cyathea smithii					4.3
Elaeocarpus hookerianus					1.5

Table 3-4 The mean total (summed values for all tiers) percentage cover per development stage of species with a total mean cover of ≥1% in at least one development stage. Values in bold type highlight dominant species which appear in the compositional part of the name of the development stage they are present in. The order of species in the table is a rough representation of species turnover along the vegetation development sequence.

Naming the plant assemblages of each development stage follows standard thesis methods. The compositional name is based on the dominant species (those in bold in Table 3.4), incorporating information about their relative abundances and tier distribution. The structural name reflects the physiognomic appearance of each assemblage.

Development stage one: [*Blechnum novae-zelandiae / Nertera ciliata*] Rockland

This stage was characterised by scattered areas of ferns (mainly *Blechnum novae-zelandiae*), shrub (mainly *Hebe salicifolia*), sedge (*Carex solandri/Phormium cookianum/ Uncinia* spp.) and grass species (*Chionochloa conspicua*) localised in areas where organic matter had remained after the landslide, or had been able to accumulate. These taller species reached on average c. 0.5 m.

Below the shrub layer was a diverse and more extensive ground layer dominated by mat forming species (*Nertera ciliata & Gunnera monoica*). However, occasional individuals of herb, shrub and tree seedling species encompassed most of the species of those growth forms that was found throughout the later development stages. In addition to the species that were found in the assemblages of later stages, there was also a significant component of herbaceous and fern species unique to this stage that favour open environments. Bare, smooth bedrock was by far the dominant ground cover.

Development stage two: *Leptospermum scoparium / Weinmannia racemosa / Blechnum novae-zelandiae* Low Forest

Stage two was characterised by a strikingly even height closed canopy reaching c. seven metres that was dominated by *Leptospermum scoparium* (manuka). On entering the habitat, a sub-canopy of tree species reaching c. four metres was immediately apparent. The sub-canopy was dominated by *Weinmannia racemosa* (kamahi) and *Nothofagus solandri* var. *cliffortioides* (mountain beech) with *Metrosideros umbellata* (southern rata) also common. These species would eventually shade out the manuka and indeed could be seen to dominate the canopies of the next two older stages.

There was a sparse but reasonably diverse layer of shrub species, typified by *Coprosma* spp. and *Pseudopanax colensoi*. This shrub layer was emergent above the overwhelmingly abundant fern *Blechnum novae-zelandiae*, which formed an even layer at c. 1.5 m. The *B. novae-zelandiae* layer shaded out the ground layer so that although there was a high diversity of mainly shrub and herb species there, each species was itself quite rare, with litter and moss dominating. Epiphyte species were just beginning to get established on the older manuka stems, with *Grammitis* spp. being most common.

Development stage three: *Weinmannia racemosa - Metrosideros umbellata / Blechnum novae-zelandiae* Forest

Stage three was characterised by a reasonably even height canopy of c. 15 m, dominated by kamahi and southern rata, with mountain beech being abundant too. Old and dying individuals of manuka still persisted in the sub canopy, however, most of the cover in this rather indistinct layer was comprised of younger individuals of the canopy species, which often merged with the lower parts of the canopy.

The small tree layer was variable in height (c. 2.5 - 4 m), quite abundant, as well as diverse, with *Nothofagus menziesii* (silver beech) being most common. *Coprosma* spp, *Myrsine divaricata, Pseudopanax* spp. and *Griselinia littoralis* were also common. There were occasional individuals of Hall's totara, and rarely miro, both podocarp species characteristic of older habitats.

The shrub layer was dominated by *Blechnum novae-zelandiae* but less so than in stage two. Other species present in the shrub and ground layer were relatively rare and mainly representative of the shrub and tree species present in the canopy and small tree layers, with the notable exceptions of the sedge *Gahnia procera* in the shrub layer and *Lycopodium* spp. in the ground layer. The ground layer was mostly covered by litter and moss. Epiphytes were common but not abundant and the diversity of the *Hymenophyllum* spp. particularly had increased from that in the previous stage.

Development stage four: *Weinmannia racemosa* - *Nothofagus solandri* var. *cliffortioides* - *Metrosideros umbellata* / *Blechnum novae-zelandiae* Forest

Stage four was reasonably similar to stage three in species composition, however there were some key features which differentiate it and indicate it being older. The most obvious feature was the increased stature (averaging c. 19 m) and cover abundance of the main canopy tree species, particularly mountain beech, which together formed a more closed canopy. Also, manuka had almost completely died out from this stage.

The small tree layer was quite tall (c. five metres) and was dominated by the species which also comprised the canopy with the major addition of silver beech and *Coprosma foetidissima*. It also had a diverse assemblage of less abundant species of lower stature mainly comprised of *Coprosma* spp., and *Pseudopanax* spp which merged into the shrub layer too. The shrub layer was diverse, with key differences compared to previous stages being a reduction in the dominance of *Blechnum novae-zelandiae*, the addition of the conspicuous forest lily (*Astelia nervosa*) and the presence of a few small individuals of the tree fern *Cyathea smithii*.

The ground layer was dominated by moss and litter, with a marked increase in moss abundance compared to previous stages. Most of the vascular species abundance was made up of tree and shrub seedlings. Epiphytes were common with the notable addition of the orchid species *Dendrobium cunninghamii*.

Development stage five: *Weinmannia racemosa* - *Nothofagus menziesii* - *Nothofagus solandri* var. *cliffortioides* / *Blechnum discolor* Forest

Stage five was immediately discernable from all the other younger stages by the tall (c. 23 m) closed canopy, the open space between the canopy and shrub layers, and the abundant crown fern (*Blechnum discolor*) characteristic of mature forests in the region. Kamahi was co-dominant in the canopy with the two beech species, southern rata was also common there.

The small tree layer was dominated by individuals of the canopy species, particularly kamahi. However, the tree fern *Cyathea smithii* and the shrub *Pseudowintera colorata* were also conspicuous. The usual species of the *Coprosma* and *Pseudopanax* genera were common, as well as Hall's totara and broadleaf (*Griselinia littoralis*).

The shrub layer was dominated by *Blechnum* spp., most notably the crown fern but was accompanied by scattered individuals of the tree and shrub species typical of higher tiers. The ground was covered by a thick layer of moss with only the occasional vascular plant such as *Nertera villosa*, *Lycopodium varium* or *Unicinia* spp. This moss carpet may have inhibited growth of tree seedlings, most of which had germinated on rotten logs.

The epiphyte layer was abundant in the higher branches and was comprised of an array of *Hymenophyllum* spp., orchids and other ferns such as *Microsorum pustulatum* and *Grammitis* spp.

3.4.2.2 Ordination – DCA & DCCA

The proportion of the total variation in species data that was explained by the first four axes of the ordination was 36.3 %. Most of this variation (78 %) was explained by the first two axes as indicated by the relative eigenvalues of all four axes (0.478, 0.152, 0.108, 0.066). Thus the third and fourth axes were ignored, as is normal practice (Jongman et al. 1995). Figure 3.7 represents floristic variation among samples with respect to the two main floristic gradients by plotting DCA axis one and two sample scores. It shows well clustered and distinct sample groups associated with each development stage. In general, there is a progression from DS 1 to DS 5 along axis one, although there is some sample overlap

among the stages. Overall sample score variability within each stage is roughly equal among stages, however there are differences among stages with respect to which axis encompasses most of the variation. The variation on axis two tends to increase with increasing age and conversely the variation on axis one tends to decrease. The gradient length of axis one (3.66 S.D.) indicates that a species turnover approaching 100 % (Jongman et al. 1995) occurs along the entire vegetation development sequence.

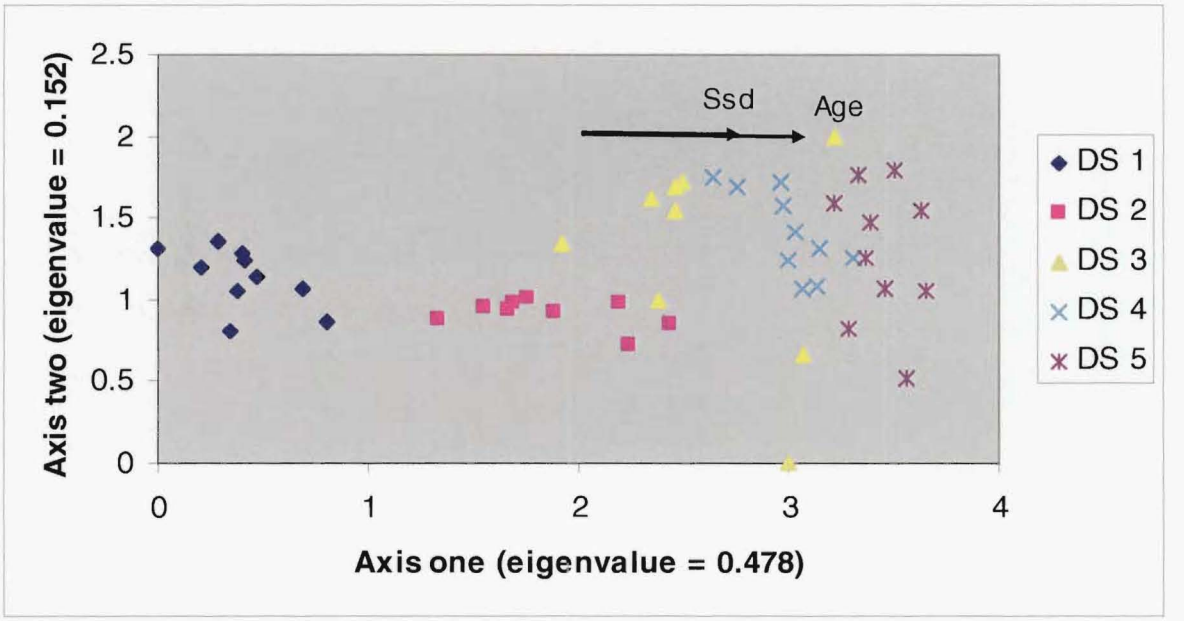

Figure 3.7 Axes one and two of the DCA ordination of the five development stages. Bi-plot vectors for environmental variables with significant ($p \leq 0.001$) correlation coefficients (r) (ter Braak & Smilauer 1998) are shown. The length of each vector is proportional to the 'r' value and the direction of the vector indicates the direction of maximum change of the continuous variable. Environmental variables: 'Age', age: 'Ssd', soft sediment depth.

The DCCA eigenvalues and gradient lengths shown in Table 3.5 are smaller than those for DCA. This is to be expected because the DCCA ordination is constrained (Jongman et al. 1995). Eigenvalues and gradient lengths of DCA and DCCA are reasonably similar for the first axis (variance explained 21.9 %), suggesting that constraining the ordination values to be linear combinations of the environmental variables included in the analysis (i.e. DCCA calculation methods) does not greatly affect the ordination. This indicates that most of the variation explained by the main floristic gradient of the unconstrained DCA ordination can be explained by the measured environmental variables.

Correlation coefficients between DCA and DCCA axis scores give further insight. There is a very strong correlation between DCA and DCCA ordination scores for axis one but axis two has a weaker correlation (Table 3.5). The result for axis one is interpreted as the main gradient of vegetation being explained very well by the environmental variables in the analysis. The result for axis two indicates that the majority of variation explained by this axis is due to unknown variables, although there is still a reasonable amount that is due to the environmental variables in the analysis. These unknown variables are not considered to be important to the overall interpretation of the dataset because DCA results show that axis two only accounts for a small proportion of the total variation in the data (6.9 %) compared with axis one (21.9 %).

	Eigenvalues		Gradient lengths		
Axis	**DCA**	**DCCA**	**DCA**	**DCCA**	**r**
1	0.48	0.28	3.66	2.22	0.97
2	0.15	0.04	1.99	0.65	0.42

Table 3-5 Eigenvalues and gradient lengths (SD) for the first two axes of the DCA & DCCA ordinations. Pearsons product-moment correlations (r) are given of the first and second DCA axes plot scores with the first and second DCCA axes plot scores.

The correlations between each individual environmental variable and DCA axis one and two are given in Table 3.6. The only environmental variables that are significantly correlated with the ordination scores of either axis are SSD and age, both with axis one.

	Correlation coefficients (r)	
Environmental variable	**Axis1**	**Axis 2**
Altitude	-0.27	0.08
Slope angle	-0.32	0.13
Aspect	0.04	0.13
pH	-0.10	-0.16
Organic carbon	-0.31	-0.15
Soft sediment depth (SSD)	0.49***	0.07
Age	0.70***	0.09

Table 3-6 Pearson product-moment correlation coefficients calculated between the environmental variables measured and the first two DCA ordination axes sample scores. '***' denotes significance at the critical value 0.439, $p \leq 0.001$, d.f=45. All data except aspect is on an interval or ratio scale.

Age is strongly correlated (r=0.70) and SSD is moderately correlated (r=0.49). The weighted correlation matrix in the DCA log file shows SSD to be also correlated with age (r=0.64). This indicates that it is not a causal factor of axis one ordination scores but stepwise regression methods discussed later are used to confirm this. Thus, since DCA axis one explains most of the variation explained by first four axes of the ordination, these results indicate that age is the major driver of floristic variation. Therefore, DCA axis one effectively represents the successional gradient and can legitimately be used as a univariate index so as to represent the successional trajectory with age.

3.4.2.3 ANOSIM

The ANOSIM results presented in Table 3.7 strongly indicate that each stage is an entity which is significantly different from its predecessor and successor; confirming what is indicated by the patterns in the DCA ordination graph (Figure 3.7). This result makes the comparison of univariate indices values among development stages a legitimate way of tracking vegetation development trajectories. The difference between the R values of each pair-wise comparison probably reflects the discrepancy in the amount of species turnover that occurs between different pairs of stages (see relative approximate median axis one position per stage, Figure 3.7). The R value of the pair-wise comparison between stages one and two shows a high level of dissimilarity, whereas the R values for the other three pair-wise comparisons indicate a good separation but with some overlap between stages (Clarke & Gorley 2001a).

Pair-wise comparison of development stages	'R' value	'p' value
1/2	0.999	0.001
2/3	0.446	0.001
3/4	0.538	0.001
4/5	0.458	0.001

Table 3-7 Results of the ANOSIM pairwise multivariate test for similarity where the null hypothesis is 'no difference between stages'.

3.4.2.4 Regression part one

When adding soft sediment depth (SSD) to the models including either DCA axis one or DCA axis two was attempted the variable was automatically rejected in both cases.

Therefore, it is concluded that SSD does not have a significant effect on floristics at the Lake Thomson site.

3.4.2.5 Univariate indices of vegetation development

Graphs showing the index response to age (means per stage with standard error bars) are presented in the regression section for most indices so that fitted curves are overlaid onto observed data. Therefore, to avoid repetition, the only indices graphed in this section are those in either Figure 3.8 (that are not presented in the regression results section due to variance problems or to no significant fit of either model occurring), or, those in Figure 3.9 (that are presented in the regression results section but only in a transformed state). Indices responses are all interpreted in the regression part two section, except for functional richness.

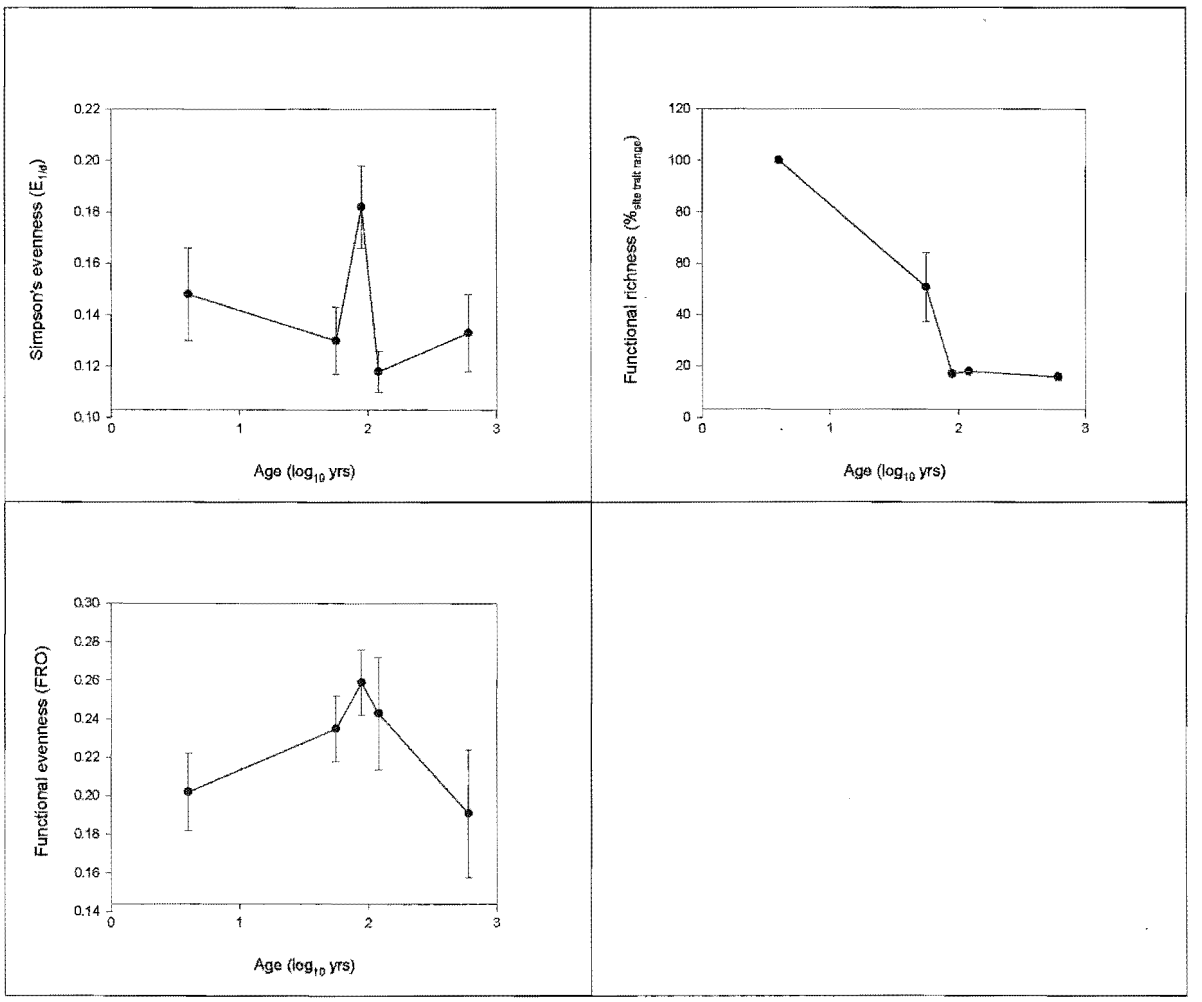

Figure 3-8 Graphs of univariate indices either unsuitable to be included in the regression analysis (functional richness) or included but not presented in that section because neither regression model had a significant fit with age (Simpson's and functional evennesses). Data points are means per development stage with standard error of mean error bars shown.

3.4.2.5.1 Functional richness

Functional richness was rejected from regression analysis because of multiple very high leverage values due to the extreme heterogeneity of variance among the stages. Even when a weighted analysis was used, error messages indicated the results were void owing to the leverage problems. Another problem with the data for functional richness was that within the highest variance stage, the values were at only two levels, rather than being spread across the range. Both these variance issues indicate a problem with the way the index calculates richness (see section 2.2.4.5.2 for further discussion of this). Nonetheless, the graph in Figure 3.8 clearly shows a very strong response of functional richness to vegetation development. The pattern is a sharp decrease followed by a levelling off in later development stages.

3.4.2.5.2 Untransformed representation of indices

The graphs of organic carbon and importance score shown in Figure 3.9 below are included here to display them on their natural axes. Results are described in the regression section.

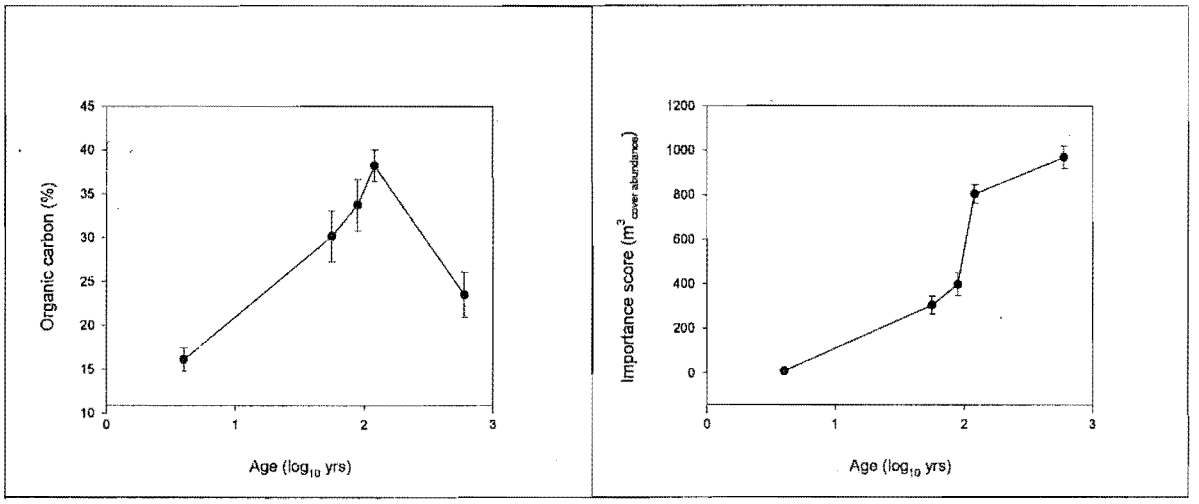

Figure 3-9 Graphs of univariate indices that are plotted in their transformed units in the regression graphs, shown here in their un-transformed units.

3.4.2.5.3 Species relative abundance distributions

Results for the ΔL test illustrated in Figure 3.11 show that in the case of this ecosystem, the development of plant assemblage relative species abundance structure does not tend towards a lognormal distribution after perturbation. Figure 3.10 below

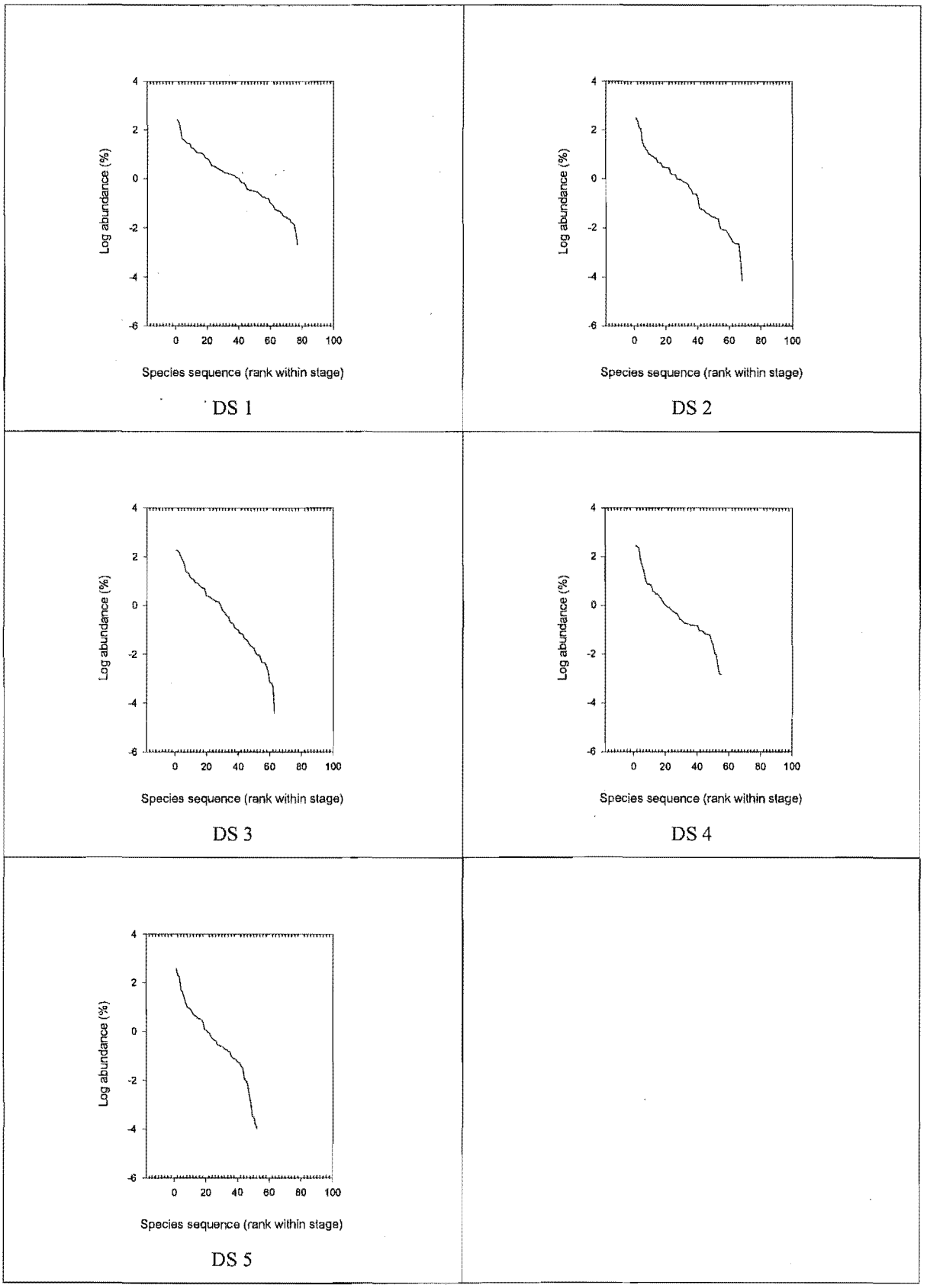

Figure 3-10 Rank/abundance plots (Log_{10} abundance versus species sequence by rank order) showing the average RAD pattern for each surface calculated by summing the abundances for each species for all the replicate samples within each surface.

complements these results. It shows clearly how the RAD changes with vegetation development. There is a progression over time from a curve that resembles the broken stick model (DS 1) model through to something closer to the lognormal model (DS 2), and, by DS 5, it is approaching the geometric series. This progressive steepening of the RAD curve signifies that as the vegetation develops at Lake Thomson, the assemblages become dominated by fewer species.

3.4.2.6 Regression part two

Results are presented in this section for the fit of univariate indices to age with either linear (Table 3.8) or polynomial (Table 3.9) regression models, as well as the F-test to discern which model fitted each index pattern best (Table 3.10).

	Linear regression results							
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{47}**	**tpr**
pH	1.27	0.028	<0.001	43.2	-0.178	0.028	-6.32	<0.001
Organic Carbon (%) *	1.28	0.027	0.003	15.8	0.104	0.024	4.30	<0.001
Importance score (m^3_{cover}) *	45.16	0.961	<0.001	88.8	3.830	0.135	28.37	<0.001
Species density (n per 100m^2)	1067.0	22.71	<0.001	46.9	-6.290	0.944	-6.66	<0.001
Simpson's diversity (-lnD)	3.42	0.074	<0.001	32.2	-0.272	0.053	-5.16	<0.001
Simpson's evenness ($E_{1/D}$)	0.11	0.002	0.495	**				
Distance from lognormal (ΔL)	3.66	0.078	<0.001	40.2	0.322	0.055	5.84	<0.001
Shannon's growth form div. (H')	2.72	0.058	<0.001	73.3	-0.555	0.043	-12.90	<0.001
Functional evenness (FRO)	0.29	0.006	0.940	**				
Functional difference (V)	138.2	2.940	<0.001	35.8	-1.651	0.161	-10.25	<0.001
Taxonomic distinctness (Δ*)	2436.0	51.82	<0.001	32.6	-7.100	1.270	-5.59	<0.001
DCA axis one (S.D.)	6.44	0.137	<0.001	89.1	1.471	0.056	26.26	<0.001

Table 3-8 ANOVA results for testing the significance of linear regressions that modelled each univariate index separately with age. '*' denotes that the variable was transformed before regression analysis '**' denotes that the intra development stage variance exceeds the variance of the inter development stage mean values; i.e. regression shows no significant relationship with age. SS=regression sum of squares, RMS=regression residual mean square, Fpr=probability calculated from the F statistic that the Y variable is dependent on the X variable based on the samples, r^2= coefficient of determination or the proportion of the total variation in the Y variable explained by the regression, Slope=regression coefficient that is the estimate of the true slope of the Y variable response to the X variable based on the samples, Slope SE=standard error of the slope estimate, t=students t statistic for testing significance of the slope (subscript number refers to the degrees of freedom), tpr=the probability that the slope estimate is does not falsely suggest the relationship between X and Y.

Graphs illustrating the observed and fitted results (Figure 3.11) are included in this section for all indices with a significant result for at least one regression model. Results tables and graphs are presented for all indices together, these are followed by an interpretation section for each individual index included in the regression analyses.

Results in Table 3.8 (Fpr) show that regression analysis found a highly significant linear trend with age for the majority of the indices. These include pH, importance score, species density, Simpson's diversity, distance from lognormal, growth form diversity, functional difference, taxonomic distinctness and DCA axis one. Organic carbon had a significant relationship with age. In all these cases, the standard error of the slope was low enough to give a highly significant probability that the slope of the fitted line is valid (tpr results). The remainder, functional evenness and Simpson's evenness, had highly insignificant relationships with age. High values of the coefficient of determination (r^2) for importance score, growth form diversity and DCA axis one signify a highly consistent linear pattern for these indices. Low values of the coefficient of determination indicate inconsistent patterns, e.g.: organic carbon, Simpson's diversity, functional difference and taxonomic distinctness. However, values have to be very low to indicate a level of inconsistency that may result in an insignificant trend.

	Polynomial regression results							
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{46}**	**tpr**
pH	1.18	0.027	<0.001	45.7	0.0908	0.052	1.76	0.085
Organic Carbon (%) *	0.71	0.016	<0.001	51.9	-0.198	0.033	-6.03	<0.001
Importance score (m^3 cover) *	35.39	0.769	<0.001	91	-0.825	0.231	-3.56	<0.001
Species density (n per 100m^2)	1044.0	22.690	<0.001	47	-1.290	1.260	-1.02	0.312
Simpson's diversity (-lnD)	3.37	0.075	<0.001	31.8	-0.062	0.073	-0.85	0.400
Simpson's evenness ($E_{1/D}$)	0.11	0.002	0.763	**				
Distance from lognormal (ΔL)	3.50	0.076	<0.001	41.4	0.1035	0.073	1.42	0.162
Shannon's growth form div. (H')	2.55	0.055	<0.001	77.4	0.108	0.062	1.74	0.089
Functional evenness (FRO)	0.26	0.006	0.096	5.7	-0.044	0.020	-2.22	0.032
Functional difference (V)	121.70	2.645	<0.001	41.6	0.788	0.316	2.50	0.016
Taxonomic distinctness (Δ*)	2433.0	52.890	<0.001	31.2	0.420	1.920	0.22	0.830
DCA axis one (S.D.)	6.08	0.132	<0.001	89.5	-0.159	0.096	-1.65	0.105

Table 3-9 ANOVA results for testing the significance of polynomial regressions modelling each univariate index separately with age. '*' denotes that the variable was transformed before regression analysis. '**' denotes that the intra development stage variance exceeds the variance of the inter development stage mean values; i.e. regression shows no significant relationship with age. Refer to Table 3.8 caption for an explanation of column headings.

Results in Table 3.9 show that all indices except for Simpson's evenness and functional evenness had a highly significant fit to a second order polynomial model. For organic carbon, importance score and functional diversity, polynomial slope significance (tpr values) and a higher coefficient of determination (r^2) than for their linear model results indicates that the trajectory was better represented by the polynomial model. A larger increase in the coefficient of determination between the linear and polynomial results for an index indicates that the fitted polynomial curve, and therefore the index trajectory, had a high degree of curvature (e.g. organic carbon). However, the F-test results below give a definitive answer as to which model fits each index best.

Index	F statistic	Fpr	Best fit model ?
pH	3.09	0.085	linear
Organic Carbon (%) *	36.38	<0.001	polynomial
Importance score (m^3 cover) *	12.70	<0.001	polynomial
Species density (n per 100m^2)	1.01	0.320	linear
Simpson's diversity (-lnD)	0.72	0.401	linear
Simpson's evenness ($E_{1/D}$)	0.08	0.779	linear
Distance from lognormal (ΔL)	2.02	0.162	linear
Shannon's growth form div. (H')	3.01	0.089	linear
Functional evenness (FRO)	4.92	0.032	polynomial
Functional difference (V)	6.24	0.016	polynomial
Taxonomic distinctness (Δ*)	0.06	0.808	linear
DCA axis one (S.D.)	2.73	0.105	linear

Table 3-10 Results of the F-test for the null hypothesis that the polynomial regression does not fit the data better than the linear regression. Rejection of the hypothesis ($p \leq 0.05$) means that the polynomial model predicts the observed index pattern significantly better than the linear model.

The F test results in Table 3.10 discern which regression model statistically fits the observed index trajectory pattern best. Thus, indices whose overall pattern is closer to linear are; pH, species density, Simpson's diversity, Simpson's evenness, distance from lognormal and growth form diversity, although, the degree of pattern linearity varies among this group. The remainder have a better fit to a polynomial model, although the curvature varies among these indices from very slight (importance score & species density) to quite pronounced (organic carbon).

A best fit result does not necessarily mean that the best fitting model is actually a significant fit, although with these data that is the case except for functional evenness.

Also, it does not indicate whether or not the index response to vegetation development is strong, or, how consistent that response is; these properties are better discerned from studying the graphs of observed and fitted values in Figure 3.11 below.

The response trajectories of each index shown in Figures 3.8 & 3.11 are described in detail in the following sections (except functional richness), however the indices can be summarised into three categories of behaviour:

1. Strong and very consistent response with a clear trend and a smooth trajectory (either fitting a linear model, or, a polynomial model with limited curvature).
    - Importance score and DCA axis one
2. Strong and consistent response with a clear trend (either fitting a linear model, or, a polynomial model with limited curvature)
    - pH, organic carbon, species density Simpson's diversity, distance from lognormal,
3. Shannon's growth form diversity, functional difference and taxonomic distinctness. Insensitive to vegetation development (no clear trend or significant fit to either regression model)
    - Functional evenness and Simpson's evenness

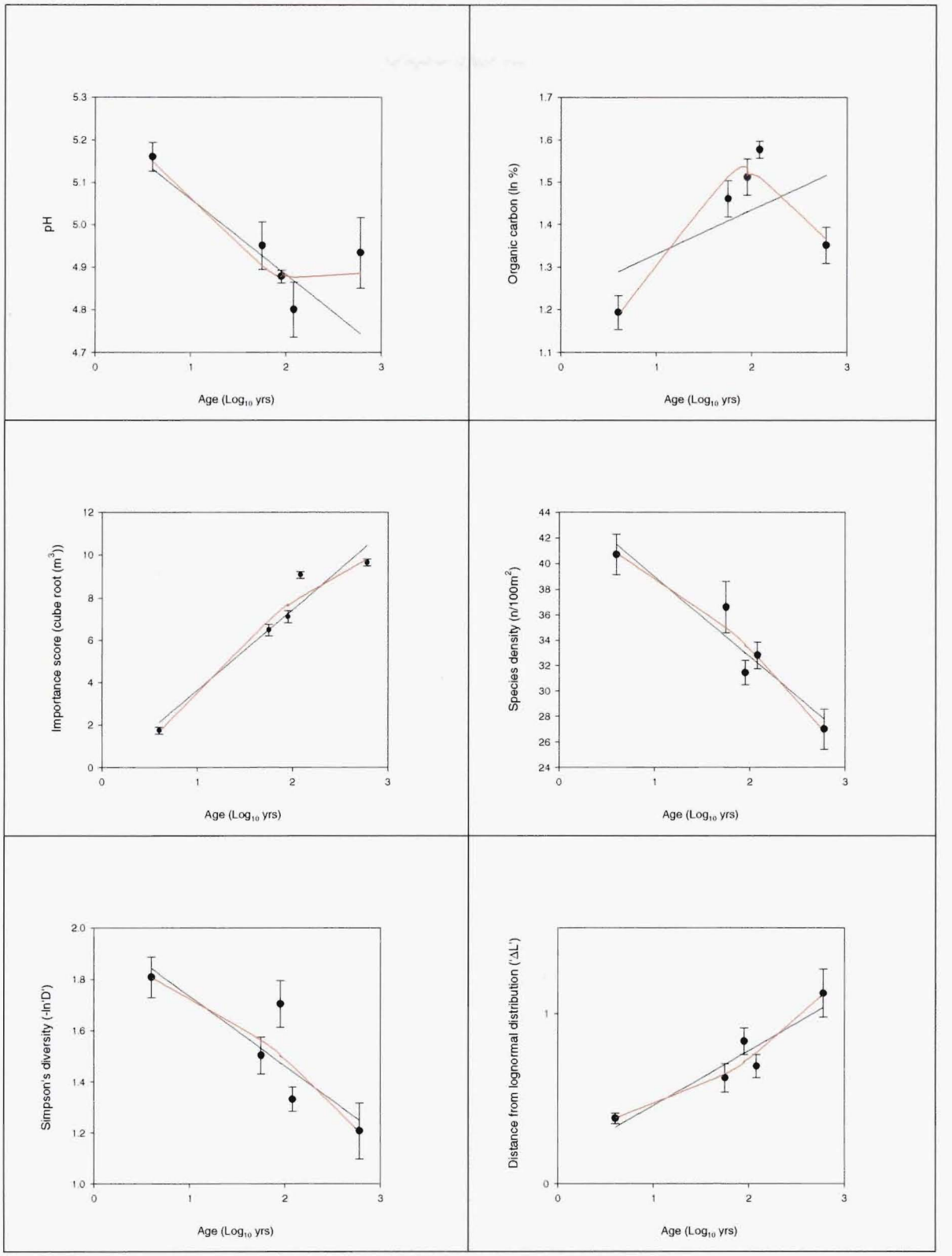

Figure 3-11 (continued on next page) Graphs showing the mean and standard error of the mean per stage for the observed data of selected univariate indices, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for whichever model(s) had a significant fit, regardless of whether the slope parameter was significant, or, whether the model was the significantly better fitting model or not. Only indices with a significant regression result for at least one model are included in this figure.

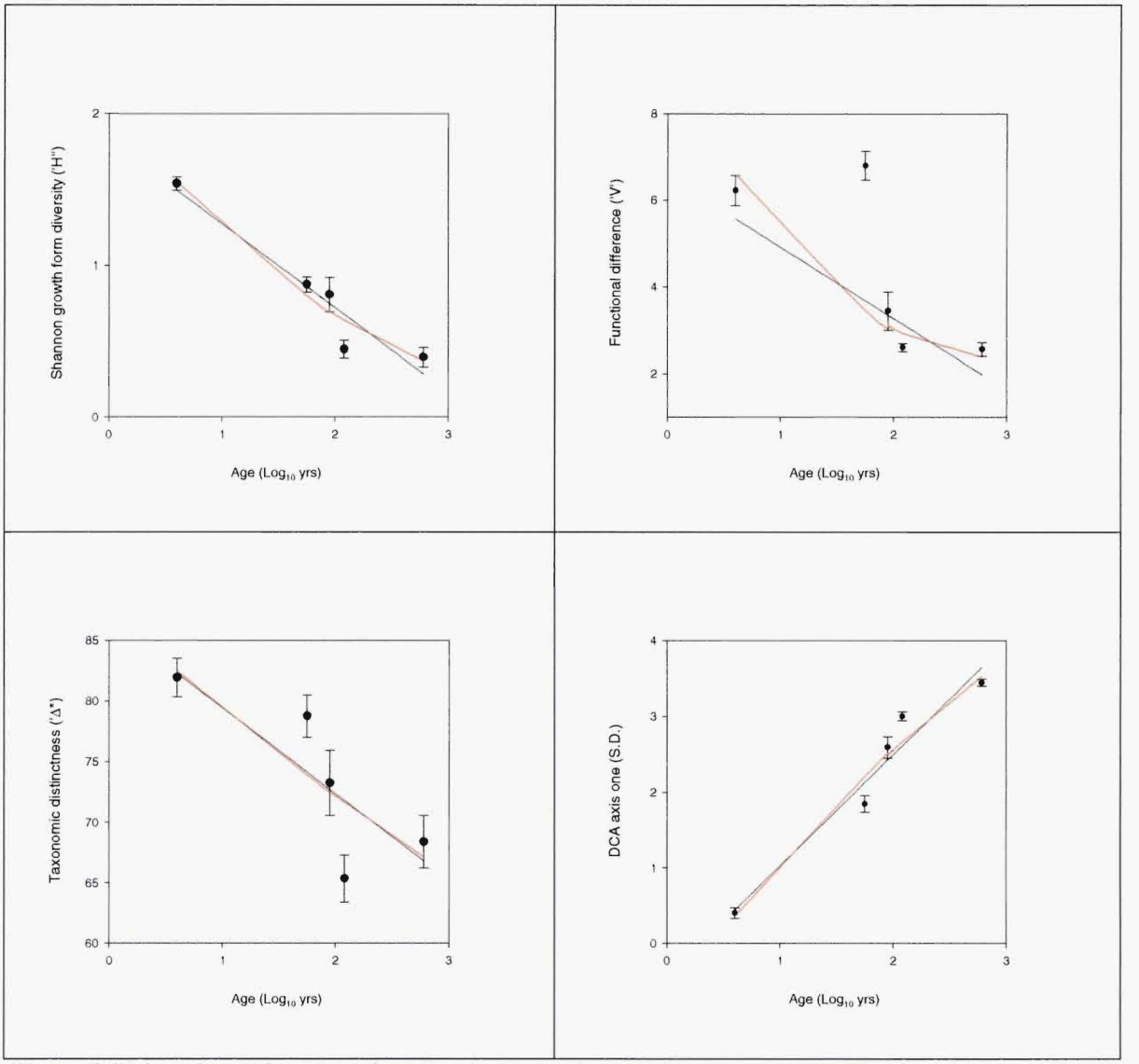

Figure 3.11 (continued from previous page) Graphs showing the mean and standard error of the mean per stage for the observed data of selected univariate indices, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for whichever model(s) had a significant fit, regardless of whether the slope parameter was significant, or, whether the model was the significantly better fitting model or not. Only indices with a significant regression result for at least one model are included in this figure.

3.4.2.6.1 Soil chemical properties

pH

pH showed a strong response with the pattern being a steady decline until DS 4, after which it appeared to increase again towards DS 5, however regression results showed that statistically the overall pattern is best described by a linear model once sample variability was taken into account.

Organic carbon

Organic carbon had a strong response to vegetation development. The pattern was a steady increase from DS 1 to DS 4 and then a decline towards DS 5 as the soil became mature. The polynomial model fitted much better than the linear model to this pattern.

3.4.2.6.2 Importance score

Importance score had a strong response to vegetation development. The trajectory showed a smooth increase with a clear levelling off at the end of the sequence.

3.4.2.6.3 Species diversity indices

Species density

Species density displayed a strong decreasing trend with age. The trajectory was close to being linear except for a minor irregularity at DS 3.

Simpson's diversity

Simpson's diversity had a strong decreasing trend with age. The trajectory was consistent with an outlier at DS 3.

Simpson's evenness

Simpson's evenness had an inconsistent and weak response to vegetation development with no clear trend.

3.4.2.6.4 Distance from lognormal distribution

The RAD distribution showed a strong response to vegetation development. Distance from lognormal increased reasonably consistently, the trajectory becoming slightly confused around the middle stages during which there was less change occurring. It appears that DS 3 was an outlier to the general pattern.

3.4.2.6.5 Functional diversity indices

Growth form diversity

Growth form diversity had a strong response to increasing age. The index decreased consistently and appeared to level off toward the oldest stages.

Functional evenness

Functional evenness displayed a weak and inconsistent response among the development stages with no clear trend across the development gradient.

Functional difference

Functional difference had a strong response to the vegetation development gradient as a whole although most of the change occurred between stages two and three. The overall trend was a levelling decrease, however DS 2 was an outlier to this.

3.4.2.6.6 Taxonomic distinctness

Taxonomic distinctness displayed a strong response to vegetation development. The overall trend was a decrease but the trajectory suggested a levelling off at the later stages.

3.4.2.6.7 DCA axis one

DCA axis one responded strongly to increasing age. The smooth trajectory showed a very consistent pattern of increase followed by a levelling off at the latter stages.

3.4.2.7 Ordination- PCA

3.4.2.7.1 PCA analysis of relationship between indices

Results illustrated in Figure 3.12 overleaf show that in combination, the univariate indices separate the samples well. The samples are loosely grouped in terms of development stage identity but there is a high degree of overlap. Nonetheless, there is a gradual progression of increasing age of samples across the graph from bottom left to top right.

Biplot arrows consist of three groups of varying tightness. The three groups are quite well separated, indicating a low correlation with one another. The groups correspond with broad type of index behaviour. The left hand group (taxonomic distinctness, growth form diversity, functional difference, Simpson's diversity and species density) all decreased with increasing vegetation development. The middle group, at the top of the graph, (Simpson's evenness and functional evenness) are those which did not show any obvious trend. The right hand group (distance from lognormal, DCA axis one and importance score) all increased along the vegetation development gradient. Within each group, the proximity of the biplot arrows corresponds with how similar the trajectories were to one another, but this does not imply that they contain the same information.

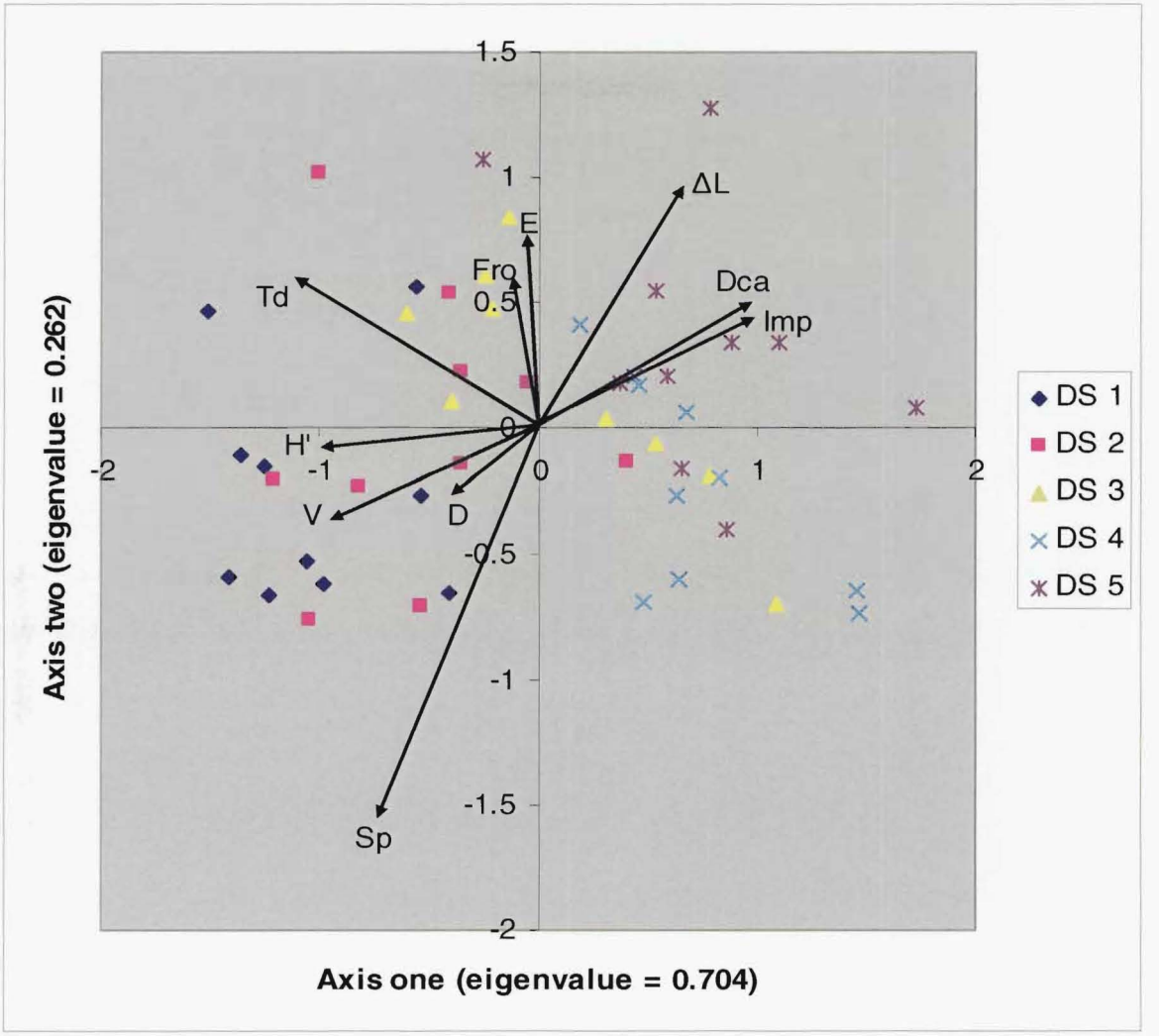

Figure 3.12 Ordination diagram of all samples based on a PCA analysis of univariate indices values. Axis one and two (shown) comprise 96.6 % of the variation in the ordination. Eigenvalues for axes 1 to 4 are 0.7037, 0.262, 0.022 & 0.010 respectively. Biplot arrows directions denote the relationship of each index to the separation of the samples, arrow length is proportional to the strength of the index's contribution to the sample variation. Key to arrows codes clockwise from the positive end of axis two: ΔL=Distance from lognormal distribution, Dca = DCA axis one, Imp = importance score, Sp = Species density, D = Simpson's diversity, V = functional difference, H' = Shannon's growth form diversity, Td = Taxonomic distinctness, Fro = Functional evenness, E = Simpson's evenness.

3.4.2.7.2 PCA analysis of successional trajectory

The first three axes of the PCA analysis depicted in Figure 3.13 overleaf account for 85.9 % of the total variation in species data. Therefore, the graph is a good representation of the vegetation dynamics that occurred along the successional gradient. The key point of the analysis is the level of trajectory complexity. It can be seen that the trajectory is simple with the final stage being a different phase than the previous four.

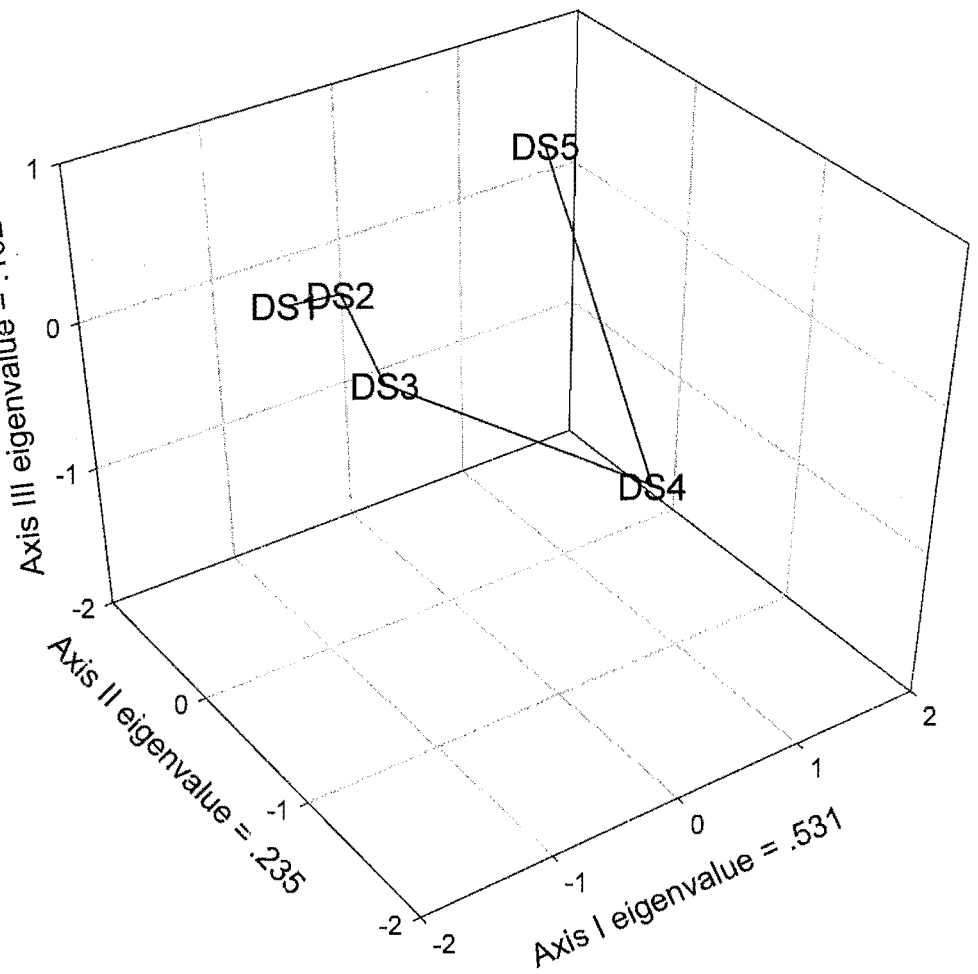

Figure 3-13 Three dimensional depiction of the successional trajectory as summarised by a PCA analysis of the species abundance data.

3.5 DISCUSSION

The main objective of this Chapter was to identify the indices that were able to clearly track the inferred vegetation development trajectory at the Lake Thomson study site. In order to address this objective, this discussion focuses on the following questions:

- Has the chronosequence method accurately inferred the vegetation development sequence that would occur under the conditions of this case?
- Can index performance & pattern of behaviour be explained by either or all of:
    - Reference to successional models and general vegetation dynamics concepts
    - Comparison to other studies of succession to forest communities after landslide disturbance
    - Comparison with patterns of other indices from this study site

3.5.1 QUALITY OF CHRONOSEQUENCE INFERENCE

DCA and DCCA results indicate that floristics were not significantly affected by measured environmental variables and that age correlates most closely with the main vegetation development gradient. The intensity of sampling within the assemblages of each stage compared to the spatial extent of the landslides suggests that a large amount of any heterogeneity that developed within each landslide, for whatever reason, has been sampled. Despite this intra-stage heterogeneity, ANOSIM results show that each stage was statistically distinct from every other stage despite three stages being quite similar in age. The development stage ages were assigned with confidence, with the first four able to be accurately aged by dendrochronology. The mature forest may be older than the estimate but this uncertainty has no great consequence on the ability of the chronosequence to infer vegetation development. This is because the pattern of development would be unaffected since the order of stages is in no doubt and also the age gap between the mature forest and the next youngest stage is large compared to the total age range of the whole sequence. Thus, the ages for the sequence are adequate for the inference of the vegetation development gradient. DCA & PCA analysis of the whole data set and regression analysis of individual indices' response suggests that the development trajectory is linear. Limited variation from this trajectory was highlighted by some indices, suggesting probabilistic processes did affect assemblage structure. However, it appears that a limited species pool is available to play the key roles in the vegetation development from a barren substrate, resulting in a largely deterministic succession.

Notwithstanding differences in sampling methodologies, the direct observation of vegetation development from 1962 to 2003 (Mark et al. 1964; Mark et al. 1989, and this study) that has been made of stages two to five provides an opportunity to confirm the accuracy of the chronosequence inference. A knowledge of the chronosequence literature suggests that this is an unusual opportunity. In general, assemblage structure appears to have been very similar among the stages at key points along the development trajectory, indeed Mark et al. (1989) assert that the claim of time being the most important factor differentiating the landslides is validated by the re-sampling this paper describes. However, stage three stands out as an exception to the rule with the earliest indicator of difference being a lower density of colonist manuka individuals than the other stages had at equivalent ages. Forty years on, the assemblage at stage three appeared to remain on a different trajectory to the other stages; it being an outlier in the inferred development

trajectory for several indices. A possible cause of this difference could have been an incomplete removal of ecological legacy by the landslide disturbance event. The relatively high floristic variation of samples for this stage displayed by the DCA analysis may also be consistent with this theory. Nevertheless, the differences are in species relative abundances rather than composition and this stage appears to be following a parallel trajectory of vegetation development to the other stages. Therefore, there is no evidence to suggest that it would not develop into an assemblage very similar to the mature forest.

In conclusion, there is nothing in the results to suggest that the chronosequence sampled in this study does not infer the general trajectory pattern of vegetation development following intense landslide disturbance in this area. Furthermore, the forest dynamics of the region (Stewart 1986) indicate that the mature forest stage of this study represents the culmination of primary succession given similar environmental conditions and would be the most stable state within a mosaic of patches initiated by frequent disturbances.

3.5.2 EXPLANATION OF INDEX BEHAVIOUR

3.5.2.1 Which model(s) of succession from the literature fit the pattern at Lake Thomson?

Despite stage one proving that all the dominant canopy species of the mature forest stage can successfully colonise within four years of the disturbance event, initial floristic composition (Egler 1954) is not a suitable model because many other species characteristic of later stages do not appear to be able to colonise under these early conditions. Likewise, relay floristics (Egler 1954) represents a rather incomplete model of the situation. The most obvious problem with the relay floristic model is that apart from the array of light demanding herbaceous species present in stage one, the vegetation development does not involve successive replacement of whole species associations. Indeed, after manuka has formed a canopy, species turnover seems to be a gradual process partially mediated by the modification of conditions owing to growth of mature forest canopy species.

The mechanism that relay floristics invokes, facilitation, is important throughout the succession. For example; early colonists *Coriaria arborea* and *Gunnera monoica* improve nutrient status of young soils (Mark et al. 1989), the manuka canopy enables more widespread recruitment of the beech species and increases avian seed dispersal, also the deeper shade provided by the closure of the beech/kamahi canopy enables understory species typical of mature forest (e.g. *Myrsine divaricata*) to flourish. However, to adopt the

facilitation model *sensu* Connell & Slayter (1977) would incorrectly assume that 'only early successional' species would have been able to establish themselves in the post disturbance environment. Nevertheless, if this strict condition is put aside, the basic Clementsian concept of reaction and autogenic processes driving the sequence (Clements 1916) that the facilitation model embodies appears to best fit the overall situation in this study site.

It is important to bear in mind though that multiple mechanisms operated within the developing assemblage simultaneously. For example; the formation of a manuka canopy probably inhibits further recruitment of manuka and other light demanding species, later on dense *Blechnum discolor* ground cover may inhibit establishment of understory individuals. Thus, species replacements are likely to have been a result of multiple mechanisms. Overlayed and interacting with these mechanisms would be a complex set of processes including competition, life history strategy, ecophysiology and resource availabilities. Therefore, a more comprehensive framework for the succession than focusing on mechanisms could be provided by Tilman's (Tilman 1985) resource ratio model, although detailed measurements of resource gradients would be required to confirm the extent of the model's validity. In reality, the relative availabilities of two resources only would be unlikely to govern species establishment and persistence entirely, but Mark et al. (1989) suggest that light availability and soil nutrient status (e.g. Nitrogen) could explain most of the dynamics.

Other studies of forest regeneration after landslides refer to a variety of models including inhibition, facilitation, Tilman's resource ratio (Nakamura 1984; Reddy & Singh 1993) and an individualistic model dependent on initial conditions and the surrounding abiotic and biotic environment (Walker et al. 1996).

3.5.2.2 Discussion of index behaviour by comparison with other information from this study site and other similar study sites

3.5.2.2.1 Soil chemical properties

The two soil chemical properties follow a similar pattern to one another in that they change in linear fashion until the final stage when they change levels, or even reverses somewhat. During primary succession soil development processes are expected to lead to the general trends observed at this study site (Walker & del Moral 2003); i.e. a decline in pH is associated with the accumulation of organic acids and a rise in organic carbon results from decomposition of carbon fixed by plant growth. There are no previous records for the

chemical properties of soils in the Lake Thomson chronosequence, however, soil profiles examined by Mark et al. (1964) indicate soils were immature until the final development stage. The continued absence of *Blechnum discolor* in the penultimate stage shown by this survey suggests that the soils of the first four stages were still undeveloped at the time of sampling because Wardle (1980b) showed this species requires well developed soils. Therefore, it seems likely that the change in soil properties at the final stage corresponds with soil maturity. The nature of the change, an apparent reversal of the trend for organic carbon and to a lesser extent pH, is unexpected though. Since a similar pattern is displayed in both indices it seems unlikely to be a sampling anomaly. A possible conclusion is that decomposition rates have declined but no explanation can be offered for this. The levelling of plant biomass towards the final stage indicated by the trajectory of importance score would have had a capping effect on volumes of litter entering the soil profile but this should not act to decrease organic carbon. Measurements of pH and organic carbon have not always been made on other landslide succession studies, with indicators of fertility such as phosphorous and nitrogen tending to be favoured. Furthermore, no landslide chronosequences that measured soil properties of any kind could be found which tracked soil development from bare bedrock, or that spanned a length of time during which soil maturity would have been reached. Nevertheless, two studies showed similar directional trends as at the Lake Thomson study site (Guariguata 1990; Reddy & Singh 1993), albeit over a short timescale compared to the predicted total length of their development trajectories. A further study highlighted that increases in soil organic carbon can lag behind other indicators of soil development (Zarin & Johnson 1995).

3.5.2.2.2 Importance score

An increase in plant abundance (as measured by importance score, cover, density or biomass) towards levels in neighbouring mature vegetation appears to be a universal pattern during landslide succession. Although no authors who gave abundance information sampled chronosequnces *sensu stricto* that included mature vegetation, some have made comment that the time taken for abundance to approach pre-disturbance levels varies. For example; in the White Mountains of New Hampshire (Francescato et al. 2001) and in the Luquillo Mountains of Puerto Rico (Guariguata 1990) it would take c. 50 years, whereas in the Blue Mountains Jamaica it would take c. 500 years (Dalling 1994). Also, fastest rates of increase did not always occur in the same phase of succession; they tend to come either early on (e.g. Smale et al. 1997; Pabst & Spies 2001) or mid-way (e.g. Reddy & Singh

1993). Previous work at the study site measuring basal area (Mark et al. 1989) indicates the same pattern of levelling biomass increase as cover abundance results from this study do. The levelling is probably a result of declining rates of productivity as the forest reached maturity (Whittaker 1975).

3.5.2.2.3 Species density

The effect of succession to forest after landslide disturbance on species diversity has not been adequately studied (Walker et al. 1996 & literature review in section 3.2.1). Most authors refer only to compositional changes and key species performance rather than tracking the response of diversity. Of those studies that were found to analyse change in diversity, all focused solely on species density. Although patterns varied, all studies reported that more mature assemblages had a higher density than early pioneer assemblages. Studies that tracked development until a mature state was reached found that towards the end of the vegetation development gradient species density levelled (Manjusha & Joshi 1990; Kessler 1999) or dropped a little from its peak (Guariguata 1990). Data from studies spanning earlier stages of development found different patterns; for example, Reddy and Singh (1993) from their study of two adjacent seres in the Himalayas showed one sere to peak quite early and another to decrease from the pioneer assemblage before increasing again, whereas, Dalling (1994) recorded a steady increase. Data from this study represent an exception to all other studies of forest vegetation development after landslides[1] because the species density increases to its peak very quickly after disturbance (four years) and thereafter declines steadily. Interestingly, data from the previous studies at this site appear to show a slightly different pattern (Mark et al. 1964; Mark et al. 1989), with the decline being reversed in the oldest stages. However, their figures are effectively species accumulation data and the point-centred quarter method used would have naturally increased total area sampled in the older habitats where individuals are more spaced out. In

[1] Data from forest successions regenerating after other types of disturbance do share this pattern (e.g. Habeck 1968; Peet 1978).

addition, plots were distributed differently to this study. This highlights the difficulties of cross-study comparisons.

3.5.2.2.4 Indices related to species proportional abundance

No examples could be found of other studies of succession to forest after landslides that investigated the proportional abundances of species, either by means of diversity indices, plotting RADs or fitting RAD models. Nonetheless, it is possible to make the broad inference from published vegetation descriptions that evenness in species abundances would tend to increase during vegetation development because early stages are usually characterised by a dominance of one or a few highly successful pioneer species. Unfortunately such inferences are not possible to compensate for the lack of direct comparative work available in the literature for the assemblage properties represented by the indices measured in this study that remain to be discussed; growth form diversity, functional character diversity, taxonomic diversity and species turnover. However, the processes behind indices patterns observed at this study site can be interpreted using the breadth of information known about the succession occurring there.

The extent of canopy species dominance and the relatively low species density of the mature forest stage at the study site are features of the beech forests of the eastern South Island of New Zealand (Wardle 1991) but many types of forest ecosystem do not share these features (West et al. 1981). The unusually high proportion of the resources that these canopy species occupy helps explain why the distance from the lognormal model of species RAD increases with vegetation development. This pattern is contrary to predictions in the literature about the lognormal distribution being typical of assemblages that are recovered from a disturbance (e.g. Preston 1962). However, Sugihara's niche division interpretation of why assemblages fit the model (Sugihara 1980) assumes a tendency towards higher diversity as assemblages develop, which is clearly not the case.

The decreasing pattern of Simpson's diversity is primarily because of the decrease in species density with age since evenness shows no clear pattern. The lack of pattern in species evenness at first seems counter intuitive considering the significant and progressive shift in the RADs across the vegetation development gradient. However, on closer inspection of the RADs it becomes obvious that the lognormal type pattern of DS 1 is no closer to even species abundances than the pattern of DS 5 that approaches a geometric series.

3.5.2.2.5 Functional diversity & taxonomic distinctness

The decrease in growth form diversity along the sequence reflects changes in character of the vegetation that would be obvious to an observing ecologist. Firstly, the loss of successional species tends to greatly reduce the importance of certain growth forms such as herbs, grasses, sedges and shrubs in the early stages. Secondly, the canopy closure that occurs between DS 3 & 4 means that assemblages thereafter are increasingly dominated by tree and fern growth forms; this shift would produce the sudden drop in growth form diversity observed between these stages.

The declining trend of functional richness is as a consequence of similar trends in high species density and richness of taxonomic groups (shown by the taxonomic distinctness index). An interesting feature of the pattern of functional richness is the discontinuity between DS 2 & 3. In common with growth form diversity, this feature of the pattern reflects successional processes. An plausible explanation would be that the loss of pioneer and light demanding species during the transition between DS 2 & 3 greatly reduces the range of leaf size present in the assemblage and hence functional richness because of their larger leaf size. The low levels and lack of pattern of functional evenness is probably linked to the similar properties displayed by species evenness.

Functional difference and taxonomic distinctness follow similar patterns, corroborating evidence in the literature that the assemblage properties the two represent are correlated (Petchey & Gaston 2002). However, differences in the patterns show the two are not directly related. The pattern similarity is interpreted as the spread of species abundance with respect to leaf area values being linked to the spread of abundance across taxonomic groups. Their declining trends are a reflection of the general decline in all types of diversity hitherto discussed (e.g. species, growth form, functional trait). Although, the increase in taxonomic distinctness between DS 4 & 5, where no other indices did, proves the ability of the index to pick up facets of assemblages that other diversity indices are insensitive to (e.g. Clarke & Warwick 1998). Close examination of species lists (Appendix five) exposes the cause of the increase to be a recruitment of species belonging to novel genera (e.g. *Schefflera digitata* & *Prumnopitys ferruginea*) that overrides the net loss of species.

3.5.2.2.6 DCA axis one

The pattern of DCA axis one indicates the typical movement of an assemblage in this environment along the vegetation development gradient. The length of the gradient is

reasonably long but being less than four S.D. units (<100 % turnover) means some species persist throughout the sequence. The fact that half of the gradient has been traversed by the second development stage indicates that rates of species turnover are much faster in the early phase during which woody species first achieve dominance and when many pioneer species disappear. The slow rates of change at the end of the development sequence adds weight to the assertion that the chronosequence has sampled a complete primary succession.

3.6 CONCLUSION

In summary, the chronosequence studied at Lake Thomson accurately infers what is a remarkably linear and deterministic pattern of vegetation development. As such, the gradient of change provides an excellent model of primary succession with which to test sensitivity of the various chosen indices. Most of the indices showed a strong response and many had consistent trajectories. The next two Chapters provide comparative gradients to investigate how closely index sensitivity and response patterns are tied to specific species assemblage structures as opposed to general successional processes.

4 GRASSLAND REGENERATION ON THE BRAIDED RIVER FLOODPLAIN OF THE GODLEY VALLEY, CANTERBURY

4.1 OVERVIEW

This chapter characterises a temperate vegetation development sequence that spans approximately 200 years and was initiated by flooding disturbance due primarily to the stochastic shifting of the rivers braids across the valley floor. The vegetation development parallels the development of the river floodplain, beginning with pioneers on unevenly sorted river sediment and ending with a diverse herbaceous community dominated by tussock grasses on a young soil.

From January to March 2003, 153 vegetation plots were sampled using a stratified random method in a six km^2 section of the upper Godley Valley, Waitaki Basin, Canterbury. Information was gathered on relative vascular plant abundance across the entire vegetation development sequence by dividing the sampling effort between five easily distinguishable development stages. The stages are considered to represent a chronosequence of vegetation development. Measurement of *Rhizocarpon* spp. lichens was used to give an age estimate for plots up to c. 40 yrs; within these plots, no measure independent of vegetation characteristics was found to be dependent on age. Consequently, plots too young or old to be aged using lichens, were categorised into broad age ranges according to previous work of other authors in similar river beds.

The main objectives of results analysis were to describe the floristic variation using multivariate methods and test the response of a wide range of univariate indices to the successional trajectory. Results show that the chronosequence method applied here is robust enough to assume that the development gradient inferred is a realistic model of succession in this environment. Discussion centres around the quality of the chronosequence and explanation of indices patterns in the context of successional processes and assemblage structure. Where possible, comparisons are made to results from previous local and international studies of succession to a herbaceous community in braided river beds.

4.2 INTRODUCTION

4.2.1 THE BRAIDED RIVER BED – A UNIQUE ENVIRONMENT

Braided rivers are uncommon worldwide, they are found in areas of active mountain uplift and erosion adjacent to valleys or plains with a shallow elevational gradient such as in north-western Canada, northern India and New Zealand (Miall 1977). In New Zealand, braided rivers are a common and characteristic feature of the eastern side of the South Island's Southern Alps. Rapid tectonic uplift along the axial ranges of the Alps during the Pleistocene, in combination with the erosive effects of glaciers and a high rainfall regime has produced high volumes of coarse sediment for transportation (Soons & Selby 1992). The upper valleys are filled with great depths of sediment and have been subject to multiple cycles of glaciation that created the characteristic 'U' shape (Soons & Selby 1992).

Where it is bounded by steep mountains, the braided river commonly occupies the entire valley floor (Reinfelds & Nanson 1993) and is characterised by a complex network of interconnected channels, with or without water, that are separated by lenticular raised bars. The bars often overlap to form larger plains but even if they become established floodplains they can never persist for long on a geological timescale (Miall 1977). The high level of spatio-temporal heterogeneity makes floodplains in general among the most species-rich environments known (Ward et al. 1999) and, moreover, they present an ideal opportunity to study succession because, in the words of Cockayne (1911, p 109), "a complete cycle of events is always in view".

4.2.2 PREVIOUS SUCCESSIONAL STUDIES ON RIVER BEDS DEVELOPING TO A HERBACEOUS COMMUNITY

An extensive literature search has produced few suitable comparisons to the study site outside New Zealand. This may be partly due to the global proliferation of dams and flood banks which have altered floodplain vegetation dynamics (Walker 1999), which in turn has limited the opportunities for study of full and natural floodplain successions. New Zealand by contrast has an unusually low proportion of its major rivers altered in this way (Williams & Wiser 2004).

The vast majority of studies on river floodplain vegetation are in systems that quickly develop a woody vegetation, including many of those on braided river beds (e.g.

Walker et al. 1986; Malanson & Butler 1991; Gibb 1994; Prach 1994; Mann & Plug 1999; Schickhoff et al. 2002) and so are not comparable to this study. Of the studies in river beds where herbaceous communities do form a major component, most do not attempt to describe inferred vegetation development. Instead they focus on how environmental factors influence plant assemblage structure and distribution (e.g. Kandus & Malvarez 2004; Sluis & Tandarich 2004).

Outside New Zealand, only two floodplain chronosequence studies that inferred development to herbaceous communities after similar disturbance regimes to that of the study site could be found. Firstly, the study by Viereck (1966) on the pro-glacial floodplain of the Muldrow glacier, Alaska infers a five stage succession where pioneer mat forming species are invaded by tuft forming grasses, shrubs then proliferate before the system reverts to a more persistent tussock and moss community. However, in contrast to the mosaic of surfaces characteristic of the Godley River bed, the development stages surfaces of the Muldrow floodplain are clearly defined contiguous terraces. Secondly, Bliss & Cantlon (1957) recognised three development stages on the Colville river floodplain in Alaska that progressed from a herbaceous to a tussock community via a woody shrub stage.

Baker & Walford (1995) studied the composition of herbaceous and shrubby communities along a six km section of the Animas river, Colorado. They did not distinguish discrete development stages but nonetheless found variation in vegetation to be correlated most highly with age or correlates of age. Their discovery of the existence of a network like pattern of trajectories with multiple stable states was explained as a series of trajectory diversions initiated by a change in abiotic conditions on surfaces owing to the effects of secondary floods. This finding highlights the need for a chronosequence experimental design in order to study vegetation development.

In New Zealand, Cockayne (1911) was the first to study vegetation development on the braided river beds when he worked in the upper Rakaia river. Later he drew upon his research in other rivers to make an extensive description of the environment and plant assemblages therein (Cockayne 1928). Foweraker (1917) recognised six 'grades' of vegetation development from the Cass river which Calder (1961) confirmed to be easily recognisable both physiographically and floristically but summarised into three stages; they both stressed the importance of fine substrate accumulation as a mechanism for facilitation of succession. More recently, Singleton (1975) categorised the terrestrial vegetation development in the Waimakariri River (near the Cass River) into five 'grades'

and was the first to attempt to put a timescale to the development. Singleton's timescale did not span as long as the chronosequence in this study does, consequently her grades divide the sequence more finely than do the development stages of this study. Burrows (1977) used his knowledge of colonisation and development rates for vegetation on multiple 'shingle surfaces near Canterbury glaciers' to attempt to put the work of Foweraker, Singleton and Calder onto a common timescale. He estimated all of the grades previously recognised to be less than 300 years old except for an old terrace, described by Foweraker, which he estimated at 1,000 years or more.

A more recent study of braided rivers in New Zealand concentrated on the formation of floodplains from a sedimentology point of view (Reinfelds & Nanson 1993) and made the most intensive effort yet to age the typical development stages. They recognised five stages in the upper Waimakariri, the descriptions of which form the basis of the stage definitions used in this study.

4.2.3 BRAIDED RIVER BED MORPHOLOGY AND LANDFORM FORMATION PROCESSES

Few studies have described the formation of braided river floodplains (Reinfelds & Nanson 1993), most concentrating on non braided floodplains. In morphological terms, the most similar described braided river system to those found east of the Southern Alps that occurs outside New Zealand is the Donjek River, Yukon, Canada (Miall 1977). Two studies of the Donjek River (Williams & Rust 1969; Rust 1972) describe a complex pattern of longitudinal bars where increasing age results in a greater height above the main active channels, fine sediment infilling and vegetation development. The morphological characteristics, substrate textural evenness and diversity, and hydrology of the floodplain typically vary along the gradient from the proximal to distal zones of the river (Rust 1972). The Godley River study site is pro-glacial and thus occurs within the proximal zone where the substrate has a greater coarse component, the braid movement is more rapid and flood

events are more violent. This contrasts with the Brahmaputra River in India, where braids are more stationary and the sediment is finer (Rust 1972).

The only study to describe the geomorphology of a New Zealand braided river floodplain in detail applies the following definition (Reinfelds & Nanson 1993, p 1114) to the Waimakariri River[1]: "a generally extensive, vegetated and horizontally bedded alluvial landform....composed of a mosaic of units at various stages of development, formed by the present regime of the river, occurring within or adjacent to the un-vegetated braids of the active river bed and periodically inundated by overbank flow".

Alpine braided river floodplains are discontinuous landforms with the most extensive floodplains commonly occurring downstream of constrictions such as tributary outwash fans and bedrock spurs (Reinfelds & Nanson 1993). The Godley study site conforms with this model; the majority of established and mature floodplain occurring downstream of the major tributary fan that is present in the site.

The morphological characteristics that the Godley study site exhibits include: varied relief (of up to c. five m), active channels, abandoned channels and scour pools, seepage channels, bars, and to a lesser extent, backswamps and aeolian dunes. For the conceptual purposes of this study, the river bed (the entire valley floor except tributary outwash fans) is divided into two zones referred to hereafter as the 'active river bed' and the 'floodplain'. Active river bed is defined as the zone of channels in which water commonly flows which covers a far greater area than that of the active channels at any time except during a flood. The floodplain encompasses the remainder of the river bed area and includes any surface sufficiently elevated or separated from the active zone so as to only receive overbank flows; the more mature the floodplain becomes, the less frequently it receives overbank flow.

Widespread floodplain stratigraphy exposure by erosional activity reveals a composite substrate throughout the Godley study site: basal rocks, cobbles and gravels are

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[1] The upper Waimakariri river is situated c. 100 km north-east of the upper Godley River and the upper sections of both rivers share a similar geomorphology.

commonly capped by accreted fines with an abrubt junction between the two layers. Often there are thin but distinct sand or gravel sheets within the basal layer. Flume experiments to model braided rivers with a high width/depth ratio similar to the Godley (Ashworth & Ferguson 1986; Germanoski & Schumm 1993) show that the size and degree of substrate sorting in forming bars is related to flood intensity and that the gravel sheets are deposited by swift overbank flows. Soons (1977) observed in the Waimakariri that the fines layer is deposited by slower moving overbank floods, and to a lesser extent by wind.

The main floodplain formation mechanisms are lateral migration of the braid train, deposition of material and channel incision; together these can construct substantial areas of floodplain which are protected from, or resistant to, erosion (Reinfelds & Nanson 1993). Whilst temporarily abandoned channels within the active river bed can support vegetation development for up to a few years, unless a significant vertical accretion event takes place to form a bar, long-term vegetation development cannot proceed (Burrows 1977). Such vertical accretion occurs by two processes in the Waimakariri River (Reinfelds & Nanson 1993); the most important is where common flood magnitudes deposit coarser material to create small and more isolated bars whilst less frequent major floods can introduce large 'slugs' of hill-slope material, creating bars up to one kilometre long. Lateral bars formed adjacent to existing floodplain margins are more likely to be stable for longer periods (Rust 1972). There is no evidence to suggest the Godley does not follow this pattern. It seems likely therefore that the derivation of surfaces upon which long-term plant succession can occur is a periodic phenomenon. However, historic records indicate that the frequency of major floods in Canterbury braided rivers (Reinfelds & Nanson 1993) is high enough for the time gap between formation of resistant surfaces to be small compared to the time scale of successional processes.

Conversely, main erosional mechanisms are lateral migration of the most active tract of the braid train, often in association with large bedload sediment waves, and reactivation of abandoned channels; in combination these can rework entire longitudinal sections of the valley within a short period of time (Reinfelds & Nanson 1993).

4.2.4 FACTORS OTHER THAN TIME AFFECTING VEGETATION DEVELOPMENT IN BRAIDED RIVER BEDS

In common with other chronosequence studies in braided river beds (Viereck 1966; Singleton 1975) it is assumed that, with judicious experimental design, all of the independent variables are relatively constant except age. A recent study of environmental

factors in the differentiation of New Zealand river bed floristics (Williams & Wiser 2004) showed water availability (as a function of annual rainfall and vapour pressure deficit) to be of primary importance. They found altitude and substrate texture to be of much lesser importance. Previous authors (Calder 1961; Reinfelds & Nanson 1993) also noted the influence of water availability but did not make any measurements. Calder (1961) linked water availability with distance from the active river bed (as a function of water table depth) and also with abundance of fines, which trap moisture more effectively than larger textures. In addition, Calder commented that an abundance of fines could also accelerate development through enabling more establishment of *Raoulia* spp. owing to their effect on nutrient availability and substrate stabilisation. Furthermore, of particular note is the historical change in species pools brought about by the spread of invasive species.

From observations throughout the field site, I drew my own conclusions about factors other than time that would possibly affect vegetation development. The texture of the substrate, apart from the abundance of fines discussed above, may have an effect on colonisation of some species and thus the early trajectory of succession but it is likely that subsequent fines accumulation would ameliorate this difference and cause a convergence (e.g. (Grubb 1986; Jumpponen et al. 1999)). The availability of propagules may vary spatially, although the majority of the species have easily dispersed windborne seed. Intensity and differential selectivity of feral mammalian grazing (e.g. from tahr, chamois and hares) may have an effect. Finally, the intensity, timing and return period of overbank flooding may be a significant influence on established vegetation. However, other authors (Cockayne 1911; Calder 1961; Burrows 1977; Reinfelds & Nanson 1993) all observed that the early stages of vegetation (up to DS 2) most likely to be subject to flooding are highly resistant to its erosional effects. They observed that plants tend to remain, holding the top layer of substrate in place, almost until the intensity is enough to rework the surface altogether. Perhaps the depositional effects of such overbank flow are more significant; it is possible that large scale and sudden addition of fines may divert the development trajectory.

This chapter investigates the first two thesis questions in the context of the data from the Godley Valley chronosequence:

I. *How do floristics vary with age and does the main floristic gradient correlate more closely with age than any other environmental variable?*

II. Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?

4.3 METHODS

The majority of the field and analysis methods are common to Chapters three and five that detail the inferred vegetation developments at the other two study sites. Common methods are described in full in the general methods, Chapter two. Only the aspects of the methods that were unique to the Godley Valley site are fully explained in this chapter; these mainly relate to the identification and ageing of development stages.

4.3.1 STUDY SITE

4.3.1.1 Site selection criteria

In order to provide an ecological contrast to the forest system at Lake Thomson studied previously, it was decided to seek a chronosequence in a grassland ecosystem. A literature search was conducted to find sites that may fit the definition of a chronosequence. It became apparent that the sub-alpine and alpine grassland ecosystems, extensive throughout the South Island, are not subject to a disturbance regime of high enough intensity and frequency to produce chronosequences *sensu stricto*. Therefore, the braided river bed ecosystem was chosen to be the only grassland system[2] suitable.

To find the most suitable valley for study, ecologists with knowledge of New Zealand's braided river beds were directly consulted (Prof. C. J. Burrows, Dr. P. Williams, Dr. P. Johnson, Dr. S. Walker, C. Woolmore), owing to the lack of published research on habitat quality and species distributions. The criteria were feasible access in combination with a relatively low abundance and diversity of exotic species. The braided river beds of

[2] It should be noted that the grassland present throughout the Godley Valley is below the timberline; thus it is actually induced grassland, resulting from an increased frequency and intensity of fires that accompanied human settlement of New Zealand.

the upper Waitaki Basin (UWB), Canterbury were quickly selected as being of most promise.

During the same period that I planned to do my fieldwork, the Department of Conservation (DoC) was conducting the first ever botanical survey encompassing all the river beds in the entire Waitaki Basin. After several reconnaissance trips accompanying DoC staff, the upper section of the Godley Valley was chosen to be the best for the purposes of this study out of the possible thirteen (Wilson 2001a) braided river systems in the UWB.

4.3.1.2 Study site description

The site is a three by two kilometre section of the riverbed of the upper Godley Valley at the eastern extremity of Aoraki-Mt Cook National Park. The location of the site within the South Island is illustrated in Figure 4.1. The co-ordinates at the north-eastern corner of the site, a position c. 200 m north-west of Red Stag hut, are: 43° 31' 50" S, 170° 29' 59" E. This particular section of the river was chosen above elsewhere because of a relatively extensive representation of the entire vegetation development sequence present in the Godley Valley river bed, and the floodplain that was relatively evenly divided between development stages.

The Godley River occupies a wide U-shaped glaciated valley bordered by steep peaks and is fed by glacial melt waters and steep side streams. The glaciers descend from the peaks of the Main Divide, reaching up to 2900 m a.s.l., into glacial lakes. The scale of the landscape is huge; from the current terminal glacial lake exits, the braided river floodplain extends for 30 km in a southerly direction with an average width of c. 2.5 km until it reaches Lake Tekapo, which itself extends for a further 25 km with it's southern edge delimited by the old terminal moraine of the receded Godley Glacier.

The two rock types present in the catchment (Gair 1967) are Torlesse Greywacke sandstone (a hard dark rock with angular grains of quartz and small rock fragments set in matrix of clay-sized particles) and argillite schist (a medium grade metamorphic rock with strongly developed crystals and easily split into planes) (Leet 1982).

The climate prevailing at the study site is temperate with cold winters and warm summers; the nearest available temperature data from the Hooker valley to the south-west (Walker & Lee 2002) quotes averages of minimum daily temperature of the coldest month and maximum of warmest month to be -4.1°C and 20.6°C respectively. Because of the higher altitude compared to that where this data is from, the study site is likely to

experience average temperatures a few degrees lower than these. Although no wind data are available, all the valleys of the UWB are renowned for their frequent, prolonged and strong north-westerly winds.

The National Institute of Water and Atmospheric research (NIWA) has a rainfall monitoring station at Eade Memorial hut, c. two km to the north of the north-western corner of the study site. This station has recorded an average rainfall of 5,400 mm per annum (1994-2002). An isohyet map (New Zealand Meteorological Service 1973) predicts a similar figure for the site of the monitoring station, but shows it to be in the middle of a very steep rainfall gradient which continues to the northern edge of the study site. The map shows the gradient to be much reduced over the study site itself (250 mm for west to east and 150 mm from north to south) with an average rainfall estimate for the site to be approximately 2,000 mm. The existence of such a rainfall gradient was observed many times during the fieldwork when westerly weather systems would deposit heavy rain within sight near the divide but virtually none would fall on the study site. The altitude of the study site increases evenly with distance up valley from its southern edge, with the range of 900–960 m a.s.l.

Vegetation within the study site is actually quite sparse with the majority of area being taken up by frequently re-worked active river bed substrate. Wilson (2001a) used remote sensing to establish that on average 17 % of the Godley River valley is vegetated. The scale of individual even aged surfaces upon which vegetation development occurs is variable but, except for the oldest surfaces, is usually no more than c. 200 square metres. These different even aged surfaces are often formed adjacent to one another to form a larger mosaic of plant assemblages.

As well as the physical disturbance regime, governed by the river flow, the vegetation of the alluvial floodplains in the Waitaki Basin has been subject to multiple types and cycles of anthropogenic disturbances (Walker & Lee 2002). It is undisputed that the increase in fire due to the arrival of the Polynesian people at around 750 BP (McGlone & Basher 1995) turned a previously largely forested landscape into induced grassland (McGlone & Moar 1998; McGlone & Wilmshurst 1999). In addition, after c. 1850, European pastoral development brought with it mammalian grazers and numerous exotic plant species (Walker & Lee 2002). However, the study site has never been actively developed for pastoralism or used for summer grazing owing to the paucity of floodplain and tributary fans that would provide grazing opportunity (Godley Peaks Station manager pers. comm. Dec. 2002).

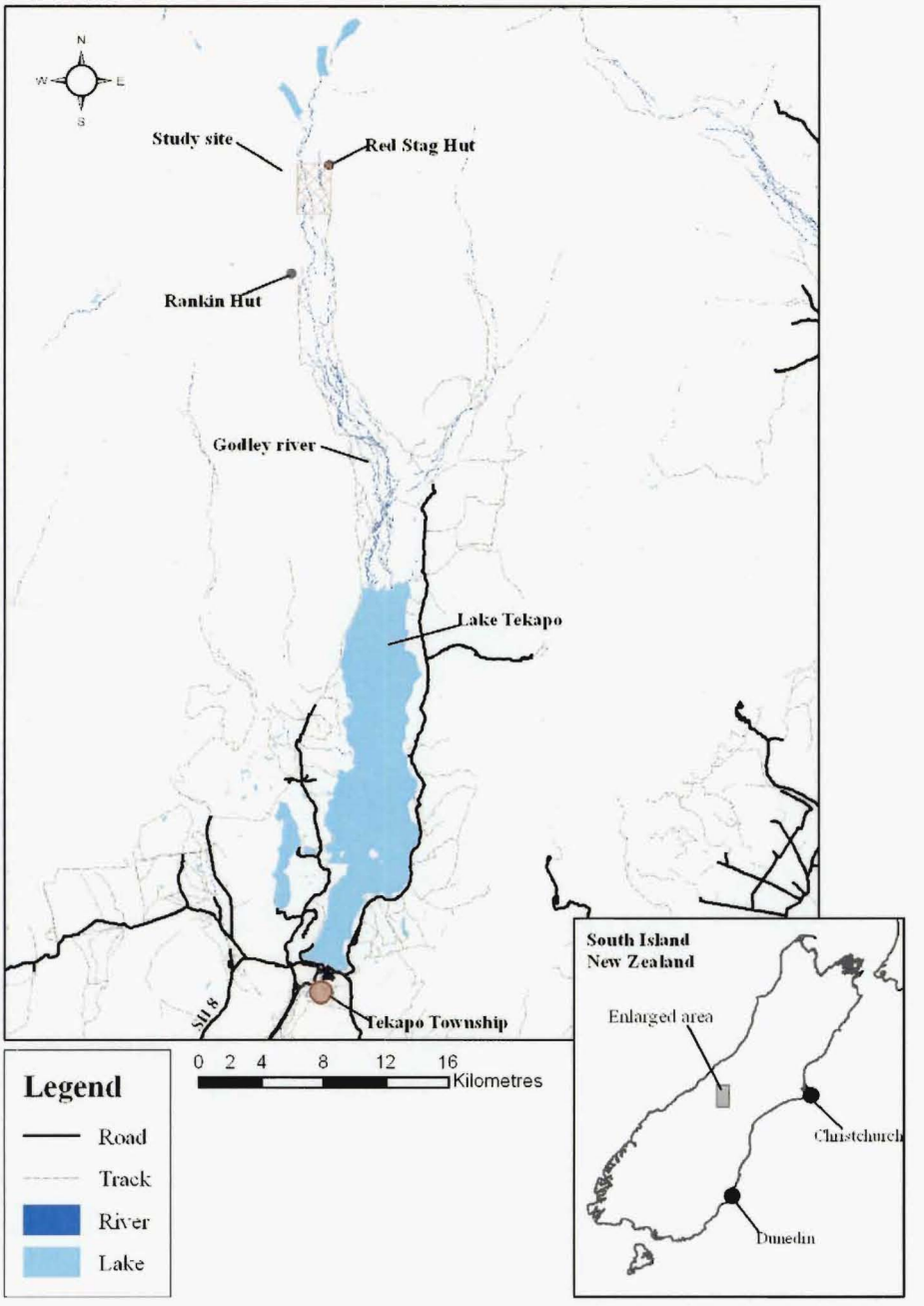

Figure 4.1 Location of the Godley valley study site within the South Island

4.3.2 FIELD METHODS

This section begins with describing how development stages were identified in the field and the sampling design employed. It continues by explaining the measurement techniques for all field data including environmental variables, plant abundances and lichen growth. Field work was carried out between January and March 2003 when plant species were easier to identify owing to the presence of their reproductive parts. Unfortunately, river flow is augmented by snowmelt and significant rainfall at this time of year which made crossings of the braids to access some parts of the floodplain hazardous.

4.3.2.1 Identification of development stages

Stages of development can be recognised in Canterbury braided river beds based on floristic and physiographic characteristics (Foweraker 1917; Calder 1961; Singleton 1975). This study uses the elements of development stage descriptions composed by Reinfelds & Nanson (1993) from their upper Waimakariri river study sites[3], that are based on fine sediment accumulation, *Parmelia* spp. lichen presence and vascular plant species presence and cover abundance. It was found that the stages described for the Waimakariri River were easily recognisable in the upper Godley[4] River and the application of Reinfelds & Nanson's system paralleled intuitive distinctions. Moreover, it was felt that any attempt at further division of the development sequence would be difficult, and, would probably lead to less floristically distinct stages.

The upper Waimakariri is considered to be an adequate analogue to the upper Godley in terms of vegetation development sequence as it is in the same climatic domain (Wilson 2001a), has similar rock types (Soons 1977), altitude, substrate texture and

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[3] Reinfelds & Nanson (1993) studied sites across an altitudinal range of between 200 and 900 m. a.s.l.; floodplain characteristics at the lower sites are distinct from the upper sites and therefore some of their development stage related information derived for surfaces at the lower sites are not relevant to this study.

[4] The final, sixth, stage is termed 'terrace' and does not exist in the study site. It appears that the upper Godley Valley is too narrow and steep sided at this point to allow the formation of such terraces because the river flow and dynamics are able to rework the entire surface of the floodplain too regularly.

landform morphology (personal observations). In addition, an ordination of alluvial grassland floristics by Walker & Lee (2002) shows the upper Waimakariri to be most similar to the Tasman valley (out of 35 valleys they studied in the eastern South Island, not including the Godley). From personal observations the Tasman Valley is very similar to the Godley in most respects, with the notable exception of a higher abundance of exotic species.

4.3.2.1.1 Development stage classification

The following descriptions are those used to classify development stage identity in the field. They are summaries of the descriptions published by Reinfelds & Nanson (1993), with some additions by myself (separated by commas and marked with *). My additions were found during reconnaissance work to be concordant with Reinfelds & Nanson's descriptions and aided development stage distinction. Flood regime detail is enclosed in brackets because it cannot be accurately assessed, and so was not directly used, but it is included as it was found to enhance the general impression of the stages.

Development stage one – 'active riverbed'

- Presently active river bed formed of channels and low braid bars, (subject to frequent reworking).
- Little or no colonising vegetation, mainly *Epilobium* spp.*.
- No lichens of any taxa colonised.

Development stage two – 'stabilising riverbed'

- Fine sediments begin to fill gaps between cobbles, though cobbles almost wholly exposed. (Over bar flow occurs frequently during discharges well below mean annual flood).
- *Parmelia* spp. lichens, mosses, *Raoulia* spp. colonising, *Epilobium* spp. abundant*.

Development stage three – 'incipient floodplain'

- Depth of fine sediment $\leq$7 cm, large stones exposed on floodplain surface, channels not infilled. (overbank flow from discharges less than mean annual flood).
- 50-100 % vegetative cover including non vascular elements.
- Large *Raoulia* spp. mats to several metres, grasses invading, matagouri seedlings present.

Development stage four – 'established floodplain'

- Depth of fine sediment 10–30 cm. Discernable channel bank separates surface from active river bed (some sites still receive overbank flow from discharges less than mean annual flood).
- Well vegetated, bare sediment only in areas of splay deposition or scour. Small matagouri, grasses more abundant than *Raoulia* spp. mats.

Development stage five – 'mature floodplain'

- Vertical relief obscured by infilling of channels with sediment, fine sediment depth from 20 cm to two metres in infilled channel braids. (Floods greater than mean annual flood needed for overbank flow).
- Dense vegetative ground cover, marked increase in exotic spp. abundance*, large matagouri up to three metres but seedlings absent.

4.3.2.2 Sampling design

The size of the study area was a compromise between obtaining a representative sample of each development stage (by including multiple disjunct surfaces of each development stage) without introducing too much climatic variation associated with distance along the main axis of the valley.

4.3.2.2.1 Plot size

Plot size was decided upon through consultation with the DoC field team who were using a plot-less method for sampling similar plant assemblages. They found that an area of approximately 25 square metres would encompass the majority of the species diversity within the most diverse assemblages. Therefore, square plots of five by five metres were used for this study.

4.3.2.2.2 Sampling effort

Owing to the lack of baseline information about the variety and diversity of plant assemblages present in the study site and also due to the variation in age within each development stage, a conservative estimate of 30 replicates per stage was decided to be sufficient sampling effort after consultation with Dr. Jennifer Brown of the Biomathematics Research Centre, Canterbury University, Christchurch, NZ.

Species accumulation curves in Figure 4.2 show two inflexions across all the development stages at around three and across most stages at around ten samples. This was taken as evidence that 30 samples was a sufficient sample size.

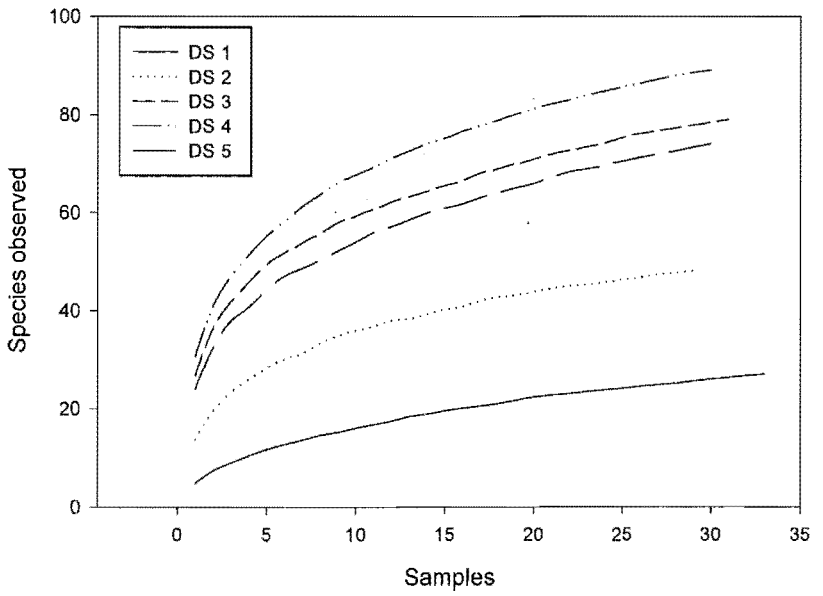

Figure 4-2 Smoothed species accumulation curves for the five development stages.

Estimates of assemblage species richness (S_{max}), using methods detailed in Chapter two, provide quantitative evidence that sampling effort is indeed adequate to characterise the species diversity of the stages. A mean of 78.3 % of S_{max} was cumulatively observed (S_{obs}) among the development stages (calculated from data in Table 4.1). The standard error of this figure (± 2.11) shows that sampling effort was relatively even among the stages, a fact also illustrated by the parallel nature of the lines representing S_{obs} and S_{max} in Figure 4.3. Proof of even sampling effort means that comparison among stages of indices related to aspects of species diversity (see univariate indices calculation methods, Chapter two) are robust.

Development stage	S_{obs}	S_{max}	S_{max} SD	proportion of S_{max} observed (%)
1	27	38	3.6	71.1
2	48	63	6.3	76.2
3	79	99	5.0	79.8
4	89	108	4.7	82.4
5	74	90	5.7	82.2

Table 4-1 Results per development stage of: 'S_{obs}' observed species area accumulation data, 'S_{max}' estimate of species richness (Jacknife 1 estimator of maximum theoretical assemblage species richness observable assuming exhaustive sampling), 'S_{max} SD' standard deviation of the species richness estimate and the proportion of S_{max} cumulatively observed.

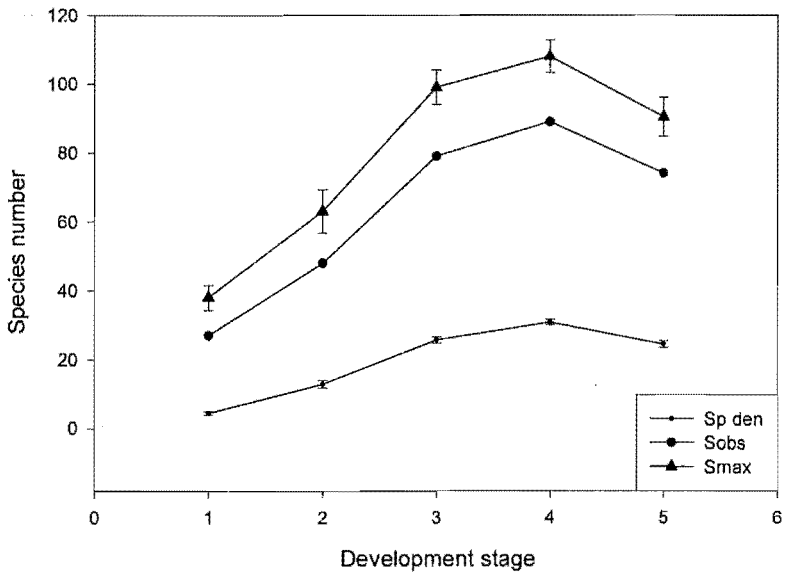

Figure 4-3 Three measures of species diversity for comparison. Sp den= mean species density (species observed per replicate sample) with standard error bars, S_{obs}= observed species richness from accumulated replicates' sample data, and S_{max}= mean estimated theoretical maximum species richness (assuming exhaustive sampling) and standard deviation bars.

Whilst the level of sampling effort achieved in the Godley Valley site is sufficient for the purposes of this study, it is worth noting that the proportion of total species richness per development stage that was sampled in the Godley is lower than in the other two study sites. This is interpreted as evidence that the spatial variation in species diversity occurs on a larger scale in the river bed grassland system than in either of the two forest systems.

4.3.2.2.3 Stratified-random sampling method

Coordinates of 300 potential plots were allocated randomly and evenly across the whole study area (c. six km^2) using the Arc-view GIS computer programme (ESRI 2003) to give a density of c. 40/km^2. Coordinates were visited at random within each kilometre square section of the study site until five samples from each development stage were made. Random visitation was ensured by using random number sheets to decide direction of travel from one point until the next and a GPS to locate the nearest potential plot in that direction of travel.

This method necessitated visiting nearly all random points to reach the target sample size in each kilometre section. This was because the majority of coordinates corresponded with sites unsuitable for sampling owing to the predominance of active river bed upon which no vegetation had developed (Figures 4.4 and 4.5 give an impression of the relative proportion of active river bed to floodplain within the study site). If a site had been free of disturbance for long enough to have vegetation then it was considered for sampling, subject to passing several criteria detailed in the following sub-section.

In this way, sites were sampled until the requisite total of 30 number of plots had been completed for development stages one, two and three, resulting in a random distribution of these plots within the entire study area. However, it was discovered that the distribution of surfaces that had reached development stages four and five was clumped into the south-eastern corner of the study site[5]. Therefore, most samples of these stages (i.e. those not obtained from the previous method) were sampled using a random method stratified at a smaller scale. This involved contiguous areas of the requisite development stage being split into 100 by 100 metre blocks and an even number of samples per block located using random number sheets to define their coordinates. Figure 4.4 shows the precise location and distribution of all the samples for each development stage within the study site. Figure 4.6 shows a typical DS 2 surface with the usual abrupt surface boundary.

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[5] It is normal to find an uneven distribution of development stages within a braided river bed (e.g. Cockayne 1911; Burrows 1977; Reinfelds & Nanson 1993).

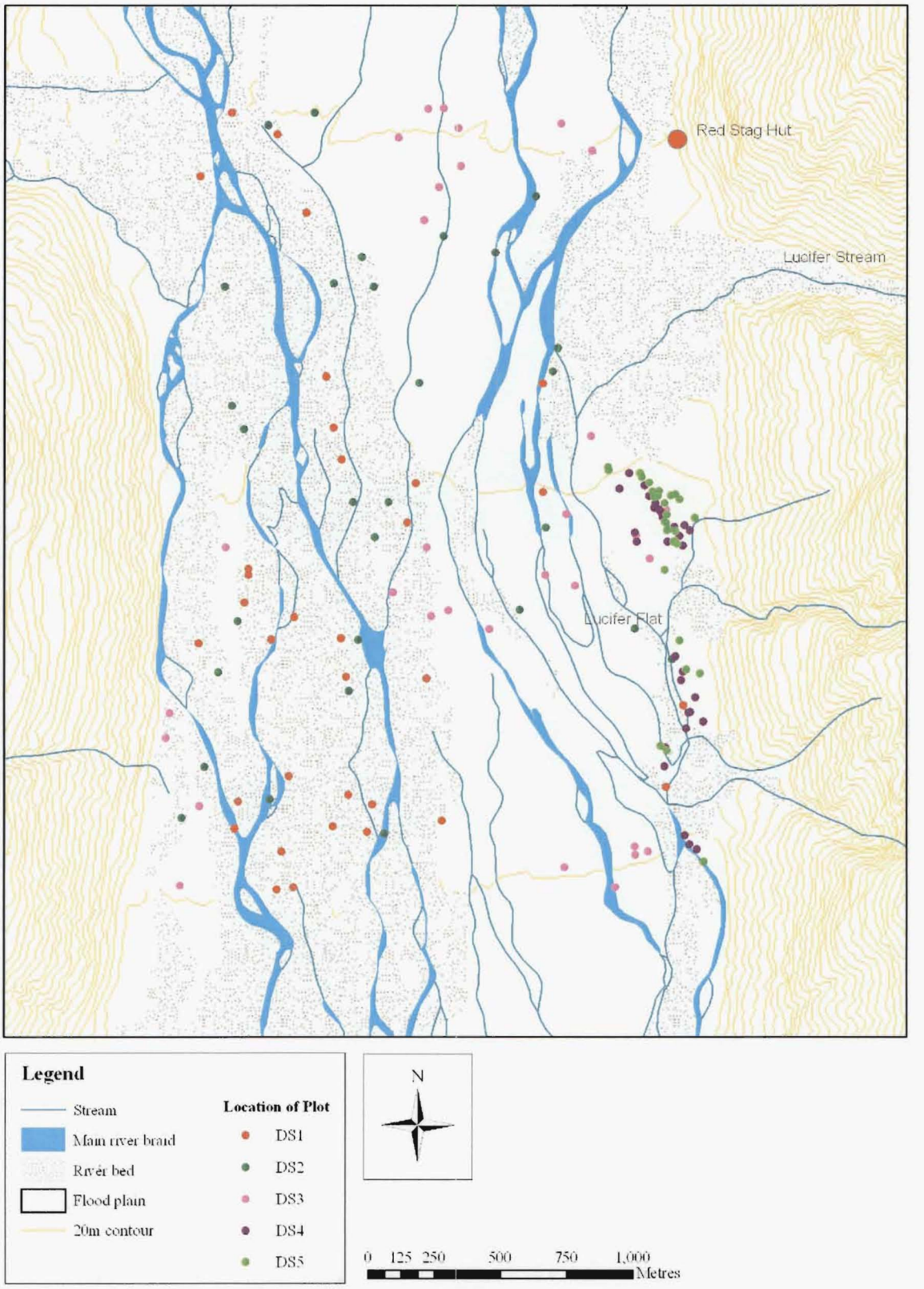

Figure 4.4 Map showing the precise location and distribution of samples for each development stage within the study site. The relative distribution of the river-bed (DSs 1&2) and floodplain (DSs 3-5) within the study site are also indicated, albeit with some imprecision.

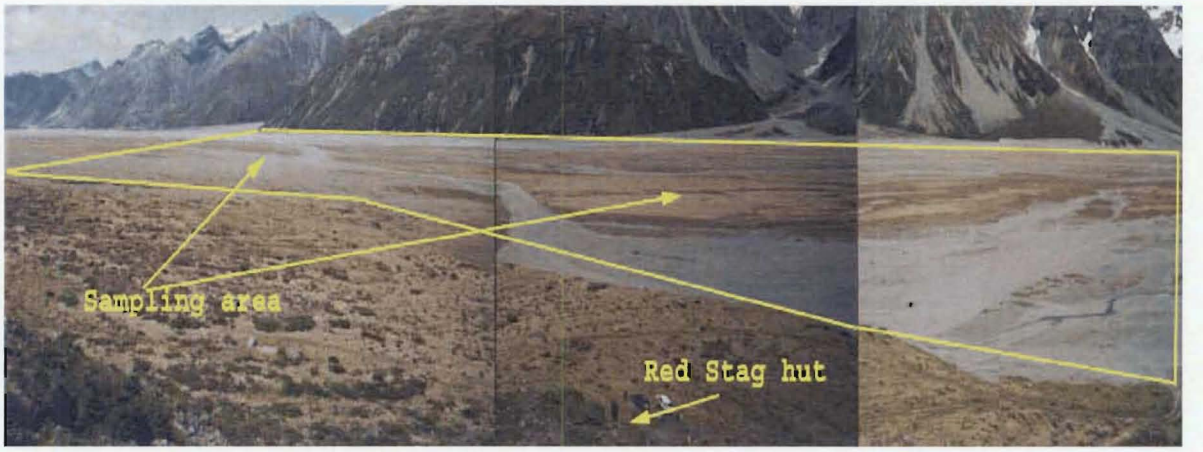

Figure 4.5 Looking southwest across the study site from above the Red Stag hut

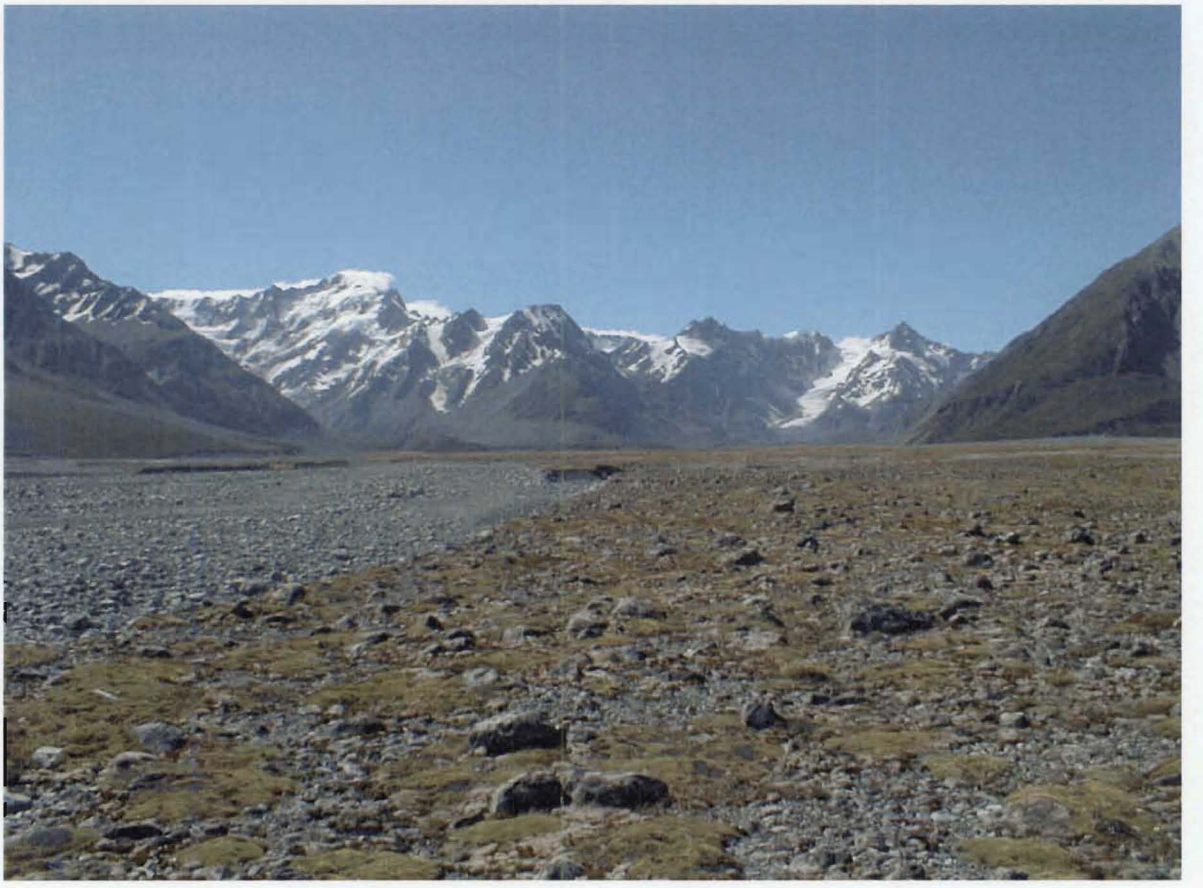

Figure 4.6 Looking north from near the southern edge of the study site with a typical late development stage two surface in the foreground and the mountains of the main divide in the background

4.3.2.2.4 Plot location criteria

The decision process for accepting a random location as a sampling unit followed a series of simple criteria. Criteria were primarily aimed at ensuring plot boundaries were entirely within an even aged surface, but another major consideration was the minimisation of edge effects from neighbouring surfaces supporting different development stages. Criteria were as follows:

- Whole plot area must consist of a similar substrate textural mixture with little surface topographical variation.
- At least 10 m distance between:
    - any two plots
    - another surface supporting a different development stage
- Plots must be placed wholly on the top surface of a bar, or forming bar. Where former channels were still distinguishable (i.e. prior to complete infilling having taken place) they were avoided.
- Good drainage (only relevant for DS 5); defined as no standing water or boggyness.

4.3.2.3 Environmental variable measurement

Altitude, slope and soft sediment depth were measured using standard thesis methods. Aspect was not recorded owing to its negligible variation over the study site.

A sketch map was drawn showing the arrangement of landform features surrounding each plot and a photograph was also taken. The proportion of ground cover was estimated in the following classes; vascular plants, mosses, lichens, litter, bare developed soil and sediment. As substrate texture is thought to be an important factor determining colonisation processes in riverbeds (Calder 1961), the total sediment cover was divided into visually estimated classes of particle size fractions after Milne et al. (1995);

- Fines = <2 mm ∅
- Gravel/coarse gravel = 2-20 mm ∅
- Pebbles = 20-60 mm ∅
- Cobbles = 60 – 200 mm ∅
- Boulders = >200 mm ∅

Then, percentage cover over the whole plot of each of the five classes was estimated.

4.3.2.4 Cover abundance estimation

Standard thesis methods involving variable tier heights were used, except that heights were able to be directly measured in the grassland habitat. Up to three tiers were identified per sample and are hereafter referred to by their nominal physiognomic names; herb layer, grass layer, shrub layer.

4.3.2.5 Plant species identification

Standard thesis methods were used to identify plants. Experience was amassed during the three weeks of reconnaissance spent working along side the DoC contract staff as they completed botanical plots throughout the Waitaki Basin. Differentiation among the species of the genera *Raoulia*, *Coprosma*, *Acaena*, *Rytidosperma* and *Epilobium* was a particular challenge to begin with.

4.3.2.6 Lichenometry

Lichen size on surface cobbles was measured using the following methods in order to provide a means to determine age for samples in the younger development stages.

4.3.2.6.1 Fixed-area largest lichen (FALL) method

The sampling method followed the FALL method of Bull & Brandon (1998). The FALL method involves measuring the longest axis (black pro-thallus rim included) of the largest yellow *Rhizocarpon* spp. lichens found in each sampling area using a flexible ruler to find the size of the largest lichen in the area. The FALL method averages out the effects of micro-scale variation of colonisation times and growth rates by using the mean figure from replicate sampling areas within each surface. The FALL method is designed to age isolated disturbance events which occur on a larger scale than the surfaces (individual bars) created in an active braided river bed. Therefore, in this study it was impossible to achieve the same number of replicate samples per surface as is recommended (100) by Bull & Brandon (1998) for the best accuracy. Instead, five samples (each covering an area of five x five metres) were taken per surface, one of which being from the plot in which the plant species abundances were measured. The remaining four samples were positioned as close to the vegetation sampling area as possible and were within the boundary of what appeared to be (by topography and vegetation development) a contiguous even aged surface.

Bull and Brandon (1998) report that to reduce variation in growing conditions among samples, sampling should only be from optimal sites, which for yellow Rhizocarpons in New Zealand's predominantly damp and cool climate are generally

considered to be on rock surfaces fully exposed to the sun and wind. However, in the study site there was a very low abundance and below average size of yellow *Rhizocarpon* spp. lichens on the exposed northern side of rocks, suggesting that in this environment their optimal growth conditions were actually in shelter from the sun and wind. Orwin (1972) sampled multiple sites in New Zealand, including one within Aoraki-Mt. Cook National Park and found that the main response of lichens to the environmental conditions is to seek the most favourable moisture conditions. It is postulated that the microclimate existing around the river bed surface rocks is much dryer than the available climate statistics suggest and around their northern side would probably be sub-optimal. Therefore, the southern aspect, being sheltered from the desiccating effects of the predominant winds, is likely to offer the optimal growing conditions within the study site. This small variation from the FALL method is not considered to bias results, because similar growth rates will be achieved by Rhizocarpons in a variety of climates via this shifting to optimal conditions, a conclusion shared by Prof. Emeritus W.B. Bull (pers. comm. April 2003).

4.3.2.6.2 Lichen taxonomy

Rhizocarpon subgenus *Rhizocarpon* are the slowest growing lichens in New Zealand (Bull & Brandon 1998). Taxa of the New Zealand yellow Rhizocarpons comprise several sections within the *Rhizocarpon* subgenus of the genus *Rhizocarpon* (Innes 1985). Each section has many species requiring laboratory identification (Benedict 1988). Bull and Brandon (1998) have shown that the two sections likely to occur in the climatic regime of the study site have similar growth rates in all growth phases. Therefore, it was considered unnecessary to attempt identification beyond the 'yellow-Rhizocarpon' level.

4.3.2.6.3 Lichen selection

Only lichens which fitted criteria aimed at accurate assessment of true thallus size were selected for measurement. The criteria were: near circular form, isolation from other lichens and clear, regular margins of the pro-thallus rim.

4.3.2.6.4 Site selection

Not all vegetation samples with *Rhizocarpon* spp. lichens present were able to be sampled using the FALL method. Only those with a high abundance of exposed rocks not sheltered from solar exposure by plant cover were chosen in order to ensure a reasonable minimum lichen abundance per FALL sampling replicate (estimated to be not less than

30). Altitude, temperature and precipitation are known to affect lichen growth (Bull & Brandon 1998); none of these vary within the study site enough to affect growth rates when compared to the variation of such conditions shown to support even growth rates by Bull and Brandon (1998). It is assumed that substrates for lichen growth were devoid of lichens at the time of surface formation because of the high energy of the river and the lack of evidence of multi-generational lichen communities within sample sites.

In practice the FALL method was only possible to implement for a narrow range of surface ages, resulting in measurements being taken from 14 DS 2 and 28 DS 3 surfaces in total. Surfaces below the younger end of the DS 2 age band were too young for any *Rhizocarpon* spp. to have become established (average colonisation time in New Zealand is six years (Bull & Brandon 1998)). Surfaces from the upper end of DS 3 age band onwards were found to have a degree of sediment and/or vegetation development which either prevented optimum growth conditions for the lichens, or, covered the rock substrate altogether.

4.3.3 ANALYSIS TOOLS

The analysis tools employed for the Godley data set are mostly the same as those used for the other two study sites. The main difference is that surface age estimation partially used lichen growth rates.

4.3.3.1 Sample age estimation

4.3.3.1.1 Lichenometry

In order to increase the accuracy of the field sampling (n=five) estimate of mean maximum lichen size per vegetation sample surface, the log-likelihood method was used to predict the distribution of an infinite number of lichenometry samples from the actual measurements taken. This method was applied with the help of my statistics advisor, Dr. Roger Littlejohn.

Following the lichenometry sampling methods described above, each surface (i=1...n) was split into five samples (subscripted by j), within each of which x_{ij}, the diameter for the largest lichen from a random[6] sample of ≥30 lichens was recorded. It was assumed that maximum lichen diameter was normally distributed within an infinite set of replicate samples (e.g. Bull & Brandon 1998), with standard deviation proportional to mean, and the same proportionality constant for all surfaces. The log-likelihood for each surface is then given by Equation 4.1.

Equation 4-1 The log-likelihood equation to estimate the largest lichen size distribution per even aged surface from a small sample size

$$L = \sum_{i=1}^{n}\sum_{j=1}^{5}\left(29\log_e \Phi\left(x_{ij};\mu_i;(k\mu_i)^2\right)+\log_e \phi\left(x_{ij};\mu_i;(k\mu_i)^2\right)\right)$$

where $\Phi\left(x;\mu;\sigma^2\right)$ and $\phi\left(x;\mu;\sigma^2\right)$ are the distribution function and probability density function, respectively, for a normal random variable with mean μ and variance σ^2.

This function was optimized numerically to give maximum likelihood estimates of k and μ_i for each surface. Values of μ_i were used as 'D' (the size of the lichen at the peak of the distribution of largest lichens from multiple samples per surface in Equation 10[7] of Bull and Brandon (1998), shown here as Equation 4.2) to back-predict the estimated plot age numerically. In this way, a more precise age estimate was produced for the plots in which lichenometry was used than could have been attained using the raw data alone.

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[6]The random element is that the sample area itself is chosen at random from the surface area owing to the random method for location of the vegetation sampling plot.

[7] There are three phases of lichen growth; colonisation, great (nonlinear) and uniform (linear) (Bull & Brandon 1998). Their Equation 10 incorporates all three and enables surfaces to be aged either if the lichens have passed through the great growth phase or if they have not.

Equation 4-2 The Bull-Brandon equation for *Rhizocarpon* spp. growth rates in the eastern South Island, New Zealand.

$$D = D_0\left(1 - e^{-K(\tau - \tau_0)}\right) + C\left(\tau - \tau_0\right)$$

Where τ is the substrate-exposure age in years, and D is the size of the lichen at the peak of the distribution of largest lichens from multiple samples per surface in millimetres. The four parameters are: τ_0 the mean colonisation time, K the nonlinear component of the growth rate during the great-growth phase, D_0 the excess lichen size produced by great growth, C the constant growth rate during the uniform growth phase. The values for these parameters are taken from table four in Bull and Brandon (1998).

Accuracy of the Bull-Brandon equation for the Godley

The Bull-Brandon lichen growth rate equation detailed in Equation 4.2 is calibrated from ninety lichenometry sites throughout the eastern side of the South Island, New Zealand (Bull & Brandon 1998). Therefore, it is considered to be applicable to the study site. Indeed, some of the younger calibration sites were braided river beds (W.B. Bull pers. comm. March 2003), and the substrate lithology, climate and altitude of the study site is consistent with calibration sites. In addition, the accuracy of this equation has been shown to be high through having been tested on areas where the timing of the disturbance event is historically recorded (Bull & Brandon 1998). Furthermore, data from the Classen Glacier' moraines (Gellatly 1982), less than three kilometres from the closest point of the study site, gives a lichen size distribution from a 100 year old site of known age that is consistent with the Bull-Brandon growth rate.

Age extrapolation beyond the age of vegetation samples able to be aged with lichenometry

Attempts were made, using linear regression, to test for dependent relationships between age and other variables for the sub-set of samples aged using lichenometry. To find those variables correlated enough with age to be suitable for dependency testing with regression, scatter graphs were used. Variables screened in this way were all ground cover and substrate characteristics as well as key species abundances common to lichenometry and older non-lichenometry plots alike. The aim was to use the regression slope of the relationship of any variables found to be dependent on age for the lichenometry aged samples to predict age using extrapolation for sites where only the dependent variable value is known. Variables tested with regression were soft sediment depth, diameter of *Raoulia* spp. mats, and abundance of key species *Festuca novae-zelandiae* and *Hieracium pilosella*. None of these variables were found to be dependent enough on age for accurate extrapolation, therefore results for these trials are not presented.

4.3.3.2 Vegetation description

Standard thesis methods were followed to characterised by three means the average plant assemblage present in each development stage. A compositional summary table is calculated, a specific name is derived and the key structural features are described.

4.3.3.3 Exploratory data analysis (EDA)

Standard thesis methods were followed for EDA. Transformations of variables prior to all multivariate analyses included importance score using the cube root (not necessary for the regressions using only the lichenometry sub-set of samples) and fines cover using the natural log.

Samples with a species density of ≤ 2 had too few values to be suitable for the algorithms of univariate indices other than importance score, DCA axis one and species density itself. Problem indices either produced a zero result or results had a spuriously high variance. Therefore, samples with a species density value of ≤ 2 for these indices were excluded from descriptive statistics, PCA analysis and regressions.

4.3.3.4 Ordination – DCA & DCCA

The floristic gradients and the effect of environmental factors upon them were analysed with DCA and DCCA ordinations in the CANOCO V4.0 computer program (ter Braak & Smilauer 1998) using standard thesis methods and options. No species were omitted from the analysis. Environmental variables included in the analysis were age (substituted by development stage), soft sediment depth, altitude (representing climatic variation) and slope. The only variables among these to be multicolinear were soft sediment depth and age, however 'VIF' values in the ordination analysis log file were not high enough to warrant the exclusion of soft sediment depth from the analysis owing to the multicolinearity. One environmental variable relating to initial substrate conditions (fines cover) was excluded from the analysis because its measurement was only possible for the early part of the sequence and correspondence analysis cannot provide correlations for sub-sets of samples.

4.3.3.5 ANOSIM

Standard thesis methods and options were used.

4.3.3.6 Regression part one

Regression analysis is used to investigate three questions pertaining to the Godley data set:

- Do selected environmental variables explain a significant amount of either of the main floristic gradients identified by DCA ordination?
- Are the univariate indices dependent on age (lichenometry sample sub-set), how strong is their response and does it follow a linear pattern?
- Are the univariate indices dependent on development stage (entire data set), how strong is their response and does it follow a pattern best described by a linear or polynomial model?

In accordance with the structure of the general methods chapter, the methods and results pertaining to these questions are split between two parts of regression analysis. The first question is covered in part one and the last two in part two. A full explanation of all methods can be found in Chapter two.

4.3.3.6.1 Testing the influence of selected environmental variables on floristic variation

Stepwise regression methods were used to test for effect on floristics of the substrate variables fines cover and soft sediment depth with the effect of age taken into account. Fines cover was selected because it was not suitable for inclusion within correspondence analysis. Soft sediment depth was selected to further test the strength of its relationship with floristics that was indicated in the ordination results by its correlation with DCA axes one and two. Both these environmental variables are partially dependent on age themselves. Therefore the rigorous testing of the effect on floristics that either of the variables might have could only be done with the sub-set of samples that were accurately aged. Standard thesis methods for stepwise regressions were followed except that homoscedascticity was ensured by checking residuals only. No transformations were necessary and Bartlett's test was not applicable because the lichenometry samples are not grouped on the x-axis.

4.3.3.7 Univariate indices of vegetation development

All of the standard list of univariate indices were calculated using standard thesis methods, except for a variation with importance score described below.

4.3.3.7.1 Importance score

In order to make the importance value for the Godley samples directly comparable to those from the Thomson and Fox forest sites, the value per sample obtained from the standard calculation method was scaled up by a factor of four to compensate for the difference in sampling area.

4.3.3.8 Regression part two

4.3.3.8.1 Fitting a linear model to univariate indices behaviour for the accurately aged subset of samples

The set of regressions used to assess the dependence of univariate indices on individual sample age as estimated by lichenometry used the standard thesis methods, except that the Bartlett's test of heteroscedasticity and concordant weighting procedures were omitted. Bartlett's test is omitted for the regression of the lichenometry data because it is designed for tests on samples that are grouped into discrete sets on the x-axis, and is inappropriate for data sets where each sample has a different value on the x-axis. In this case, the regression analysis assumption of homogeneity of variance was met by analysing the residuals of a trial run, removing any outlying samples[8] and re-running the analysis without them. Any values with a high leverage were particularly scrutinised because the scarcity of values at the upper end of the x axis scale of this data set makes the regression results more sensitive to leverage effects. No indices vales were transformed for this analysis.

4.3.3.8.2 Fitting linear and polynomial models to univariate indices variation among development stages

Standard thesis methods and options were employed for the set of regressions used to examine indices change with time over the whole chronosequence. Those samples with a species density of ≤ 2 (eight samples in total) were removed from all analyses (resulting in n=145) because they had spurious values for many indices, owing to the formulae not being designed for such low diversity. In addition, some samples were removed from three

[8] Heterosedasticity caused 3 samples to be omitted from the importance score data set, five from the functional richness dataset (these are interpreted in the discussion), and one from the distance from lognormal data set (which has no ecological interpretation). High leverage caused two additional samples to be omitted from functional richness only.

indices owing to having large residuals or a high leverage effect[9]. No indices, except for importance score, were transformed before analysis.

In order to use regression analysis to examine change of a dependent variable among groups of samples, the independent variable (i.e. the x axis, in this case age) must be measured on a quantitative scale. Therefore, the median of the estimated age ranges for samples within each development stage shown in Table 4.2 were used as the best estimate for development stage age. Methods for deriving the age ranges are presented in section 4.4.2.1.2. Although these ages are not precise, it is certain that successive stages correspond with increasing age. Moreover, this is proposed to be a sufficiently accurate method for the purposes of the thesis objective to examine response of indices to general trends of vegetation development.

Development stage	Estimated age (yrs)
1	2
2	8
3	26
4	95
5	200

Table 4-2 Estimated ages per development stage derived from the medians of the estimated age ranges for samples within each development stage.

Bartlett's test results in Table 4.3 overleaf show that over half the indices required a weighted analysis in order to satisfy the assumption of homoscedasticity.

[9] Functional richness had 6 outliers removed, two of which had a high leverage effect. Taxonomic distinctness had 4 outliers removed, all of which had a high leverage effect. Importance score had 3 outliers removed, none of which had a high leverage effect.

	Bartlett's test results		
Univariate index	χ^2	**'p' value** (d.f. =4)	**Requires weighting?**
Importance score (m^3_{cover})*	10.00	0.04	N
Species density (n per $25m^2$)	23.68	<0.001	Y
Simpson's diversity (-lnD)	36.25	<0.001	Y
Simpson's evenness ($E_{1/D}$)	29.36	<0.001	Y
Distance from lognormal (ΔL)	63.34	<0.001	Y
Shannon's growth form diversity (H')	45.93	<0.001	Y
Functional richness ($\%_{site\ trait\ range}$)	2.56	0.633	N
Functional evenness (FRO)	12.18	0.032	N
Functional difference (V)	43.54	<0.001	Y
Taxonomic distinctness (Δ*)	4.95	0.293	N
DCA axis one (S.D.)	30.7	<0.001	Y

Table 4-3 Results of Bartlett's test for homogeneity of variance for all indices with the development stage data-set. '*' denotes that a transformed version of the variable was used in the test. The critical value for rejection of homogeneity of variance was $p \leq 0.001$.

4.3.3.9 Ordination - PCA

Standard thesis methods and options were used for both the species and indices based analyses that used the PCA method.

4.4 RESULTS

The results follow a logical order and duplicate the order in the methods section.

4.4.1 FIELD DATA

4.4.1.1 Environmental variables

The data for environmental variables are presented in Figure 4.7 overleaf. Cover was measured for categories of substrate texture other than fines but these are not considered important determinants of floristic variation, so are not presented here or at any other stage.

Altitude variation is reasonably constant among the development stages. There is a slight bias to the southern half of the study area (<930 m) owing to the relative lack of samples in the northern half (see Figure 4.4 also). Slope decreases slightly among the development stages due to the accumulation of sediment over time tending to reduce the

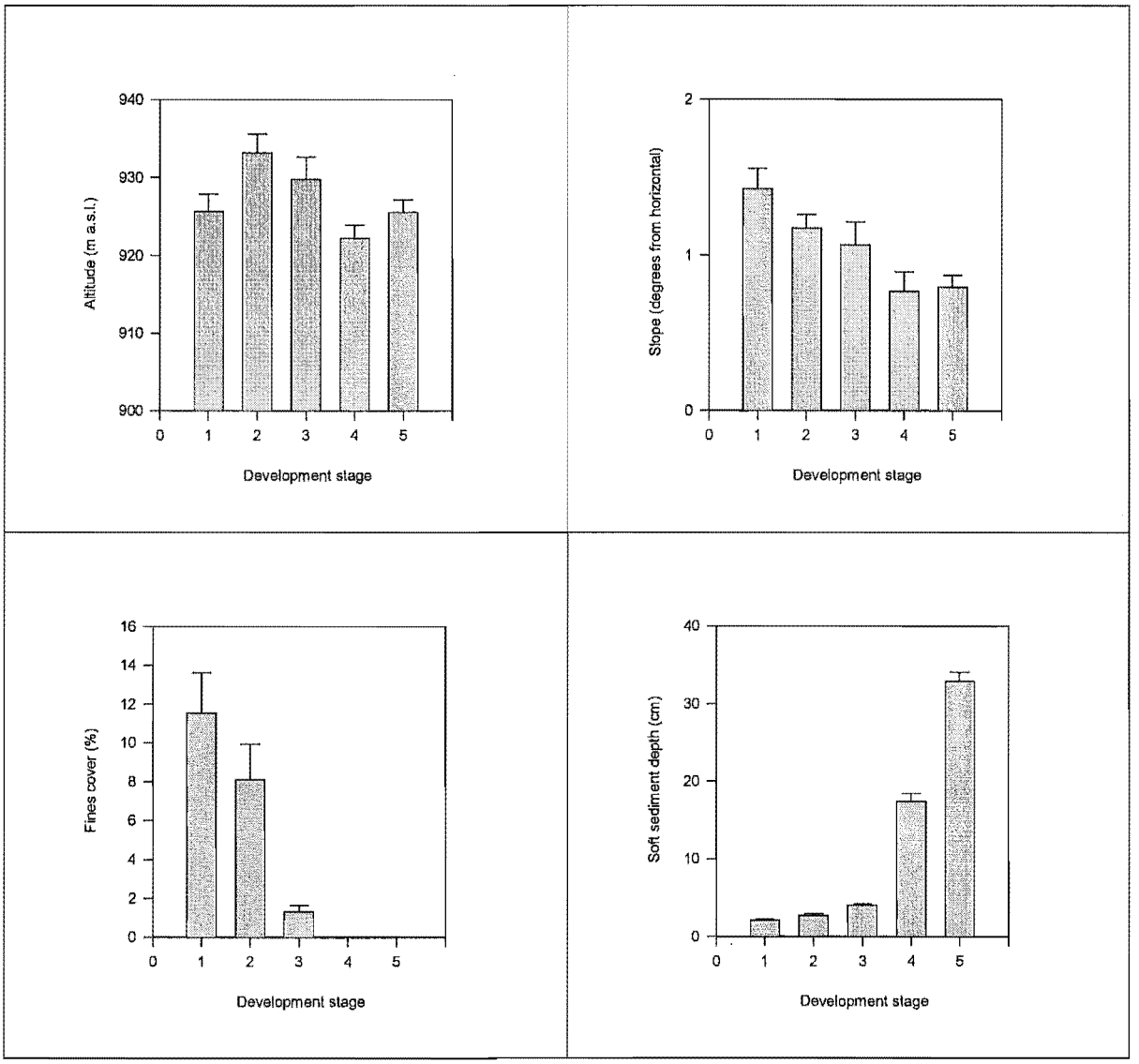

Figure 4-7 Bar graph representation of the summary statistics for selected environmental variables.

natural slope of the valley floor. Fines cover tracks the development of vegetative cover and is inversely related, with a marked reduction between DS 2 & DS 3 corresponding with the time when many species are expanding rapidly. The key result for fines cover is that there is substantial variation about the mean, particularly for DS 1 which could affect

conditions for colonisation[10]. Soft sediment depth is even within each development stage, reflecting even surface topography of the original bar upon which sediment has accumulated. The depth increases exponentially with development stage, but this is probably approximately linear with respect to time.

4.4.2 RESULTS OF ANALYSES

4.4.2.1 Sample ages

4.4.2.1.1 Lichenometry ageing

Lichenometry techniques enabled a total of 42 samples to be aged with a range of estimated age from 7-36 years. The spread of ages among samples is biased towards the younger end of the range owing to progressive accumulation of sediment tending to reduce exposure of lichen-bearing substrate from about 25 years onwards. The maximum age of 36 years derived correlates well with unpublished results of W.B. Bull of more extensive lichen measurements in similar braided systems in New Zealand where he was unable to derive an age of >40 years, also because of sediment accumulation (Prof. Emeritus W.B. Bull pers. comm. 2003).

4.4.2.1.2 Development stage age ranges

The development stages designated in the field have been assigned approximate age ranges following the practice of previous studies in New Zealand braided river beds (e.g. Singleton 1975; Burrows 1977). The most recent and thorough attempt at ageing braided river bed development stages local to the study site is that of Reinfelds & Nanson (1993). They combined measurements of sedimentation rates, interpretation of time series aerial photography and dendrochronology of the matagouri shrub (*Discaria toumatou*) to give an age ranges estimate to each development stage.

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[10] However, regression tests (section 4.4.2.5.1) with the *Rhizocarpon* aged subset of plots strongly indicated that this variation in fines cover did not affect floristics.

These age ranges are used as the basis for ageing the development stages at the study site. This is based on the assumption that changes in the variables used to identify the development stages (vegetation cover, depth of fine sediment and *Parmelia* spp. lichen colonisation) occur at similar rates in the two valleys. Lichenometry ages obtained in this study have been used to calibrate ages to fit the development rates in the study site for the group of stages (DSs 2-4) which contained any lichenometrically aged samples. Table 4.4 details both the ageing schemes.

Development stage	Reinfelds & Nanson age Range	Modified R & N age range calibrated for the study site	Number of samples	Median sample age
1	0-3	0-3	33	2
2	3-30	3-13	29	8
3	30-50	11-40	31	26
4	50-150	40-150	30	95
5	150-250	150-250	30	200

Table 4-4 Comparison of development stage ageing schemes used in the Waimakariri (Reinfelds & Nanson 1993) with the modified version used in this study. The number of samples taken in each stage is noted.

Explanation of the calibrations to Reinfelds & Nanson's development stage age ranges

The minimum *Parmelia* spp. colonisation time of three years defines the boundary between DS 1 & 2. Since *Parmelia* spp. presence/absence was used as a criterion for differentiation of these stages in the field there is no need to change this age range boundary.

All lichenometry plots fell within stages two and three. Age ranges for these stages were set by the range of ages for the samples originally designated to be in each stage from field classifications (section 4.3.2.1.1). Therefore, the small overlap in lichenometry ages that exists between these stages (DS 2 & 3) indicates a good match between development stage identity and age.

Results in Table 4.4 show that the lichenometry ageing technique used in this study produced a substantially lower minimum age estimate for DS 3 than that given by Reinfelds & Nanson (1993). The lichenometry technique is considered to produce more accurate age estimates for samples than the techniques used by Reinfelds & Nanson (1993). Therefore, this study indicates that early stages of vegetation development (up to

and not including DS 3) in eastern South Island braided river beds can proceed faster than previously thought. Furthermore, the small discrepancy between the minimum age estimates for DS 4 samples given by this study and the study by Reinfelds and Nanson suggests that development rates during the phase encompassed by DS 3 are slower than was previously thought.

The three plots in DS 3 with no lichenometry age all had too limited rock exposure owing to sediment accumulation to provide sufficient sample size for the FALL method. However, they were all noted to have had largest Rhizocarpons of a similar size to the oldest lichenometry plot (36 years). It is assumed that all these plots are older than the oldest lichenometry plot because of their greater amount of sediment. Therefore, these samples are estimated to be c. 40 years old and this provides the upper limit of for DS 3. None of the DS 4 plots contained any fully exposed *Rhizocarpon* spp. thallii at all, therefore, they were all assumed to be older than any plots in DS 3. Thus the lower limit for DS 4 is set as the upper limit for DS 3.

Matagouri growth rates from Waiamakariri sites (Reinfelds & Nanson 1993) are the basis of the remaining age boundaries. The upper limit of DS 5 (250 years) is below the minimum age (350 years) at which matagouri is likely to have disappeared through senescence and lack of replacement of old individuals (Reinfelds & Nanson 1993). This is because none of the matagouri individuals present on DS 5 surfaces were judged to be near senescence. Their disappearance is an important diagnostic characteristic for older terraces (e.g. Calder 1961) than appear to be present in the study site. A study by Dobson & Burrows (1977), suggested that a vegetation physiognomy like that of DS 5 (sparse clumps of matagouri in a 'savannah-like' grassland) is in the order of 200 years. This further corroborates the age range for DS 5 given in this study. In addition, Reinfelds (1991) suggests that almost all of the valley floor for the upper Waimakariri is capable of being reworked by the river within 250 years, based on rates of erosion measured from aerial photography. This estimate for reworking of the Waimakariri River is the same as that of c. 250 years for the braided Donjek River, Alaska (Williams & Rust 1969). There is no reason to suggest that the upper Godley would be any different from these, therefore the upper limit of 250 years for DS 5 would seem sensible.

4.4.2.2 Vegetation description

In this section, the plant assemblages of each development stages are named and described. First though, the sequence of vegetation development is summarised.

Vegetation development in the braided river bed begins with a sparse assemblage of herbaceous clump and mat forming pioneers. These are gradually accompanied by an increasing diversity and abundance of herbaceous species, tuft forming grasses and rushes, short tussock grasses, mat forming and dwarf shrubs, and seedlings of erect shrubs. This assemblage forms a first successional phase and increases in abundance and stature until it out-competes mosses and lichens and the substrate is entirely covered by vascular species. The second phase is characterised by the invasion and eventual domination of sward forming and tall tussock grasses with scattered individuals of taller shrub species gradually reaching maturity. At this point, or before, as must happen over most of the area of the river bed, a river braid migrates to re-work the surface and return the sequence to the start. However, even if surfaces were not reworked, forest species would be unlikely to invade owing to the prevalence of hard frosts that tend to occur during winter inversion layers (D. Norton pers. comm. 2003).

Table 4.5 overleaf summarises vegetation development in terms of the composition of species assemblages and the relative abundances of their constituent species.

Species name	Development stage 1	2	3	4	5
Epilobium melanocaulon	**0.27**	1.6			
Raoulia hookeri	**0.01**	**1.9**	2.1		
Raoulia haastii		**2.5**	**8.2**		
Rytidosperma setifolium		**1.2**	1.4	1.2	
Discaria toumatou			**5.2**	3.0	2.5
Leucopogon fraseri			4.2	9.3	2.5
Luzula rufa var. *albicomans*			1.8		
Rytidosperma buchananii			1.1		
Poa colensoi			**2.3**	**16.2**	15.6
*Hieracium pilosella**			1.8	8.2	3.1
Festuca novae-zelandiae			1.8	**32.0**	**47.0**
Coprosma atropurpurea			1.2	9.5	2.0
*Agrostis capillaris**				14.5	**20.1**
*Anthoxanthum odoratum**				14.4	**30.5**
*Trifolium repens**				10.2	**23.7**
*Holcus lanatus**				7.8	**22.1**
*Hieracium praealtum**				6.5	5.1
*Linum catharticum**				6.1	1.3
Muehlenbeckia axillaris				3.1	
Hydrocotyle novae-zelandiae var. *montana*				1.7	1.2
Cerastium fontanum subsp. *vulgare**				1.7	2.7
Acaena fissistipula				1.1	
Hypericum perforatum *				1.0	1.2
Helichrysum filicaule					1.2
Poa cita					1.0

Table 4-5 The mean total (summed values for all tiers) percentage cover per development stage of species with a total mean cover of ≥1 % in one development stage or more (Owing to the sparse cover in DS 1 a cut off of 0.01 % was used for this stage only). Values indicated by bold type highlight dominant or characteristic species (in any tier) which appear in the compositional part of the name of the development stage they are present in. The order of species in the table corresponds to a rough representation of species turnover through the chronosequence. '*' denotes an exotic species.

The following names and vegetation descriptions for each development stage have been elucidated using the tiered abundance information that is summarised in the table above as well as supplementary notes made in the field. Each name has two parts which represent the composition and structural appearance respectively. Full details of methods including the significance of coding used in the names can be found in Chapter two.

4.4.2.2.1 Development stage one : {*Epilobium melanocaulon - Raoulia hookeri*} Stonefield

This stage was characterised by an extremely sparse cover of young individuals of pioneer herbaceous species reaching up to 10-15 cm. Species density was generally low but reached up to ten. Pioneer species included several species of willow-herbs (*Epilobium*

spp.), the mat forming *Raoulia* species, *Muehlenbeckia axillaris*, and delicate tuft grasses and rushes such as *Lachnagrostis lyallii* and *Luzula rufa* var. *albicomans*.

4.4.2.2.2 Development stage two: [*Raoulia haastii - Raoulia hookeri - Rytidosperma setifolium*] Stonefield

The species characterising this stage were mostly the same pioneer species as in the previous stage, but had achieved a greater cover, most notably so the *Raoulia* species which often coalesced to form mats up to one metre in diameter. However, vascular vegetation was still sparse, with the total cover abundance being <10 %. There were a greater range of grasses (including *Rytidosperma* spp.) and herbs (e.g. *Stellaria gracilenta*, *Hydrocotyle novaezelandiae*, *Wahlenbergia albomarginata*), able to colonise because of the increased shelter provided by the presence of pioneers as well as the greater accumulation of fine sediment.

The grasses and more developed patches of willow-herbs together formed the beginnings of a second tier (up to 20 cm), above the ground hugging species. Encrusting lichens of the *Parmelia* genus and moss (mainly *Racomitrium* sp.) appear to have spread fast, helping to stabilise the substrate.

4.4.2.2.3 Development stage three: [*Discaria toumatou / Raoulia haastii – Poa colensoi*] Mossfield

Development stage three was typically characterised by the dominance of moss cover, and although there was considerable variation among samples in the total amounts of vascular and moss cover, bare substrate was on average only c. 20 % of the cover. The species density and growth form richness was much higher than previous stages with a high abundance of mat forming (e.g *Leucopogon fraseri*, *Coprosma* spp.) and low growing (*Pimelia* spp.) shrubs. The tussock forming grasses, *Poa colensoi* and *Festuca novaezelandiae,* were fairly common.

Most of the vegetation was still small in stature with a dominance of mat forming species interspersed with small grasses and herbs; only the occasional tussock reached over c. 30 cm in height. *Raoulia* spp. mats were still common and sometimes very large (up to c. two metres diameter) but were beginning to senesce and were thickly invaded by grasses, rushes and matagouri (*Discaria toumatou*) seedlings. Exotic species, most notably the pasture grasses *Anthoxanthum odoratum* and *Agrostis capillaris*, as well as some herbs (e.g. *Rumex acetosella* and *Hypericum performatum*) were common in some samples.

4.4.2.2.4 Development stage four: *Festuca novae-zelandiae* / (*Poa colensoi*) Tussockland

Development stage four was characterised by an open canopy of tussock grasses (mean height c. 45 cm) with the occasional and conspicuous emergent matagouri shrub up to c. 1.5 m. Vascular plants formed over 90 % cover with the remainder comprised of mainly moss and litter.

Although tussocks dominated by cover abundance and visual impression, there was a high diversity of inter-tussock plants including most of the herbaceous species and all of the shrub species of earlier stages, with the notable addition of the charismatic Compositae herbs (*Helichrysum* spp.), taller shrubs (*Gaultheria* spp. and *Coriaria* complex), and the spreading exotics *Trifolium* spp. & *Hieracium* spp. *Raoulia* species were still present between the tussocks but were dying out. Exotic grasses had increased in abundance and diversity by this stage (cf. DS 3) with the addition of *Holcus* spp., but the plant community was predominantly native if measured either by species diversity or cover abundance.

4.4.2.2.5 Development stage five: *Festuca novae-zelandiae - Anthoxanthum odoratum - Holcus lanatus - Agrostis capillaris / Trifolium repens* Grassland

This stage was totally dominated by grasses where the exotic species formed a thick even height sward between the taller native tussocks of *Festuca novaezelandiae*, *Poa colensoi*, *Poa cita* and *Festuca matthewsii*. By cover abundance, the exotic grasses were a little more common than the native tussocks. There was a reduction in overall species density at this stage (cf. DS 4) that was probably associated with the inhibition herbs and shrubs by the thick, continuous grass layer (mean height 45 cm). Matagouri shrubs comprised a lower proportion of the total plant importance than in DS 4 but were approximately equally abundant with DS 4. Matagouri seedlings were no longer present. *Raoulia* spp. had disappeared and the inter tussock ground layer was dominated by the invasive weeds *Hieracium* spp. and *Trifolium* spp., although native species were still common. A thick (up to c. 50 cm) layer of fine sediment had accumulated which was too young to have developed a profile of differentiated soil layers but its dark colour indicated a high organic content.

4.4.2.3 Ordination – DCA & DCCA analyses

DCA ordination is used to graphically represent the pattern of floristic variation among and between development stages as well as to establish if age is the strongest correlate with the primary gradient of floristic variation. The graph of DCA axis one and

two values for each sample in Figure 4.8 shows a distinct clustering for each development stage despite the existence of some overlap. Results in Table 4.6 show that axis one represents a long gradient of species turnover (gradient length = 5.2), equating to c. 1.5 complete cycles (i.e. 150 %) (Gauch et al. 1981; Jongman et al. 1995). There is a non linear gradient in the amount of species turnover encompassed within each development stage, with a marked increase until DS 3 followed by a decrease toward DS 5, which has the least of all.

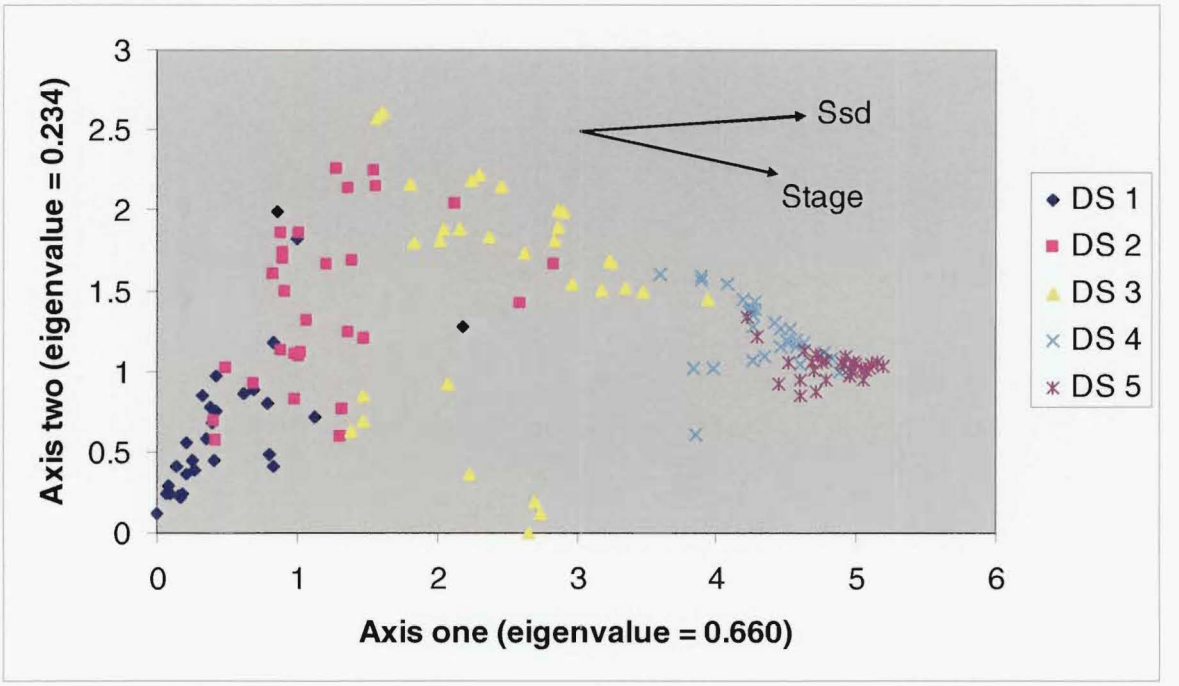

Figure 4.8 Axes one and two of the DCA ordination of all samples' species abundance data. Biplot vectors for environmental variables with significant ($p \leq 0.001$) correlation coefficients (r) (ter Braak & Smilauer 1998) are shown. The length of each vector is proportional to the 'r' value and the direction of the vector indicates the direction of maximum change of the continuous variable. Environmental variables: 'Stage'= Development stage; 'Ssd'=soft sediment depth.

The eigenvalues of the four unconstrained DCA axes from one to four are: 0.660, 0.234, 0.166, & 0.120 respectively. These equate to 27.1 % of the total variation within the species data being accounted for by the first two axes, compared to 35.8 % by the first four. Thus, axes three and four are ignored for the purposes of ordination interpretation because they are relatively unimportant; the ecologically relevant information being displayed by the first two (Jongman et al. 1995) and the main floristic gradient being represented by axis one.

Axis	Eigenvalues		Gradient lengths		r
	DCA	DCCA	DCA	DCCA	
1	0.66	0.51	5.20	4.59	0.99***
2	0.23	0.06	2.61	2.36	0.03

Table 4-6 Eigenvalues and gradient lengths (SD) for the first two axes of the DCA & DCCA ordinations. Pearson product-moment correlations (r) are given of the first and second DCA axes plot scores with the first and second DCCA axes plot scores. '***' denotes a highly significant result at the critical value $p \leq 0.001$; d.f. 152.

The first and second DCA axes gradient lengths and eigenvalues in Table 4.6 are similar to those for DCCA except for the eigenvalues for axis two. This indicates that constraining the ordination to be a linear combination of the environmental variables included in the analyses (ter Braak & Smilauer 1998) affects the main axis of variation very little, and that the variation associated with axis two is probably associated with unmeasured environmental variables. Furthermore, results in Table 4.6 show the sample values for the first axis of DCA and DCCA to be very highly correlated, suggesting that no environmental variables of significant influence on the major axis of variation exist beyond those included in the analysis (Jongman et al. 1995). In contrast, the extremely low correlation between DCA and DCCA sample values for axis two emphasises the discrepancy between their eigenvalues and reinforces the conclusion that the variation explained by axis two is due to unmeasured environmental variables (Jongman et al. 1995).

Correlation coefficients in Table 4.7 show that development stage is the most highly correlated variable with DCA axis one (r=0.82). The other environmental variable

Environmental variable	Correlation coefficient r_p/r_s	
	Axis1	Axis 2
Altitude (r_p)	0.03	-0.13
Slope (r_p)	-0.26	-0.11
Soft sediment depth (r_p)	0.74^{***}	-0.32^{***}
Development stage (r_s)	0.82^{***}	-0.24

Table 4-7 Correlation coefficients calculated between the environmental attributes measured and the first two DCA ordination axes plot scores. Pearson product-moment (r_p) correlation scores critical value 0.257 $p \leq 0.001$ d.f. 149 given where data is of a quantitative scale and Spearman's rank (r_s) critical value 0.307 $p \leq 0.001$ d.f. 149 given where data is of a nominal scale. '***' signifies significance at the critical value.

significantly correlated with axis one is soft sediment depth (r=0.74). However, correlation tables in the DCA ordination output log show that soft sediment depth is significantly correlated with development stage (r=0.855). This suggests that the correlation of soft sediment depth with axis one is a function of its relationship with development stage. Soft sediment depth is also significantly negatively correlated with axis two (r=-0.34). Axis two is not correlated with development stage, thus it is assumed to represent a component of floristic variation that is independent of sample age. Therefore, the correlation of soft sediment depth with axis two indicates that variation in soft sediment depth does cause floristic variation among samples of similar age. Nonetheless, since axis two is of relatively minor importance and the correlation is weak, the effect of soft sediment depth is not considered to confound the vegetation development trajectory inferred by the chronosequence to a great extent. Thus, in conclusion axis one represents mainly a gradient of increasing development stage, so it is reasonable to assume that age is the main driver of floristic variation at this site. This conclusion supports the use of DCA axis one values as a univariate index to represent the successional gradient.

4.4.2.4 ANOSIM

The results for the analysis of similarities (ANOSIM) test (Table 4.8) show a highly significant result for each pair-wise comparison meaning that each stage has floristics that are statistically different from its successor and predecessor. This result justifies the treatment of each development stage as a separate entity for the purpose of comparison among stages of results of the univariate indices because the ANOSIM test is based on the same species abundance data set as all of the indices.

Pairwise comparison of development stages	'R' value	'p' value
1/2	0.524	0.001
2/3	0.513	0.001
3/4	0.815	0.001
4/5	0.312	0.001

Table 4-8 Results of the ANOSIM pairwise multivariate test for similarity where the null hypothesis is 'no difference between stages'.

The 'R' value enables the results for each pair-wise test to be distinguished from each other since, unlike the 'p' value, it is an absolute measure of group separation (Clarke

& Gorley 2001a). Using the interpretation thresholds suggested by Clarke and Gorley (2001a), stages three and four (R=0.815) can be termed 'well separated' and all the other comparison pairs come under the 'overlapping but different category'. Stages four and five though are clearly the least separated as can also be seen from the graph of DCA ordination axis one and two sample scores (Figure 4.8).

4.4.2.5 Regression part one

4.4.2.5.1 Testing the influence of selected environmental variables on floristic variation

Soft sediment depth was found to have a weak but significant relationship (p=0.028, d.f.39) with the floristic gradient represented by DCA axis two within the lichenometry aged sub-set of samples when the effect of age was taken into account. This significance level corresponds with explaining just under 10 % of the variation that remained unexplained after age was taken into account. There was no such significant relationship of soft sediment depth with the gradient represented by DCA axis one when age was taken into account. Fines cover had no significant effect on either floristic gradient.

4.4.2.6 Univariate indices of vegetation development

Observed results (mean per development stage and standard error bars) for all univariate indices are presented in Figure 4.12 (in regression part two section), with their fitted response trajectories overlaid. Only importance score results are presented in this section as well (Figure 4.9 below), so that they can be seen in their untransformed state.

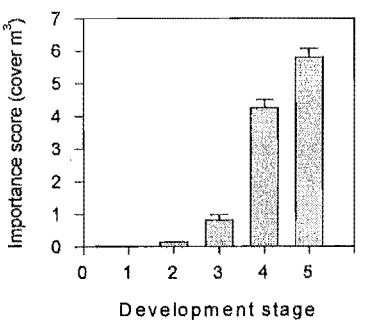

Figure 4-9 Untransformed mean and standard error per development stage for importance score (the only index that was transformed for regression analysis).

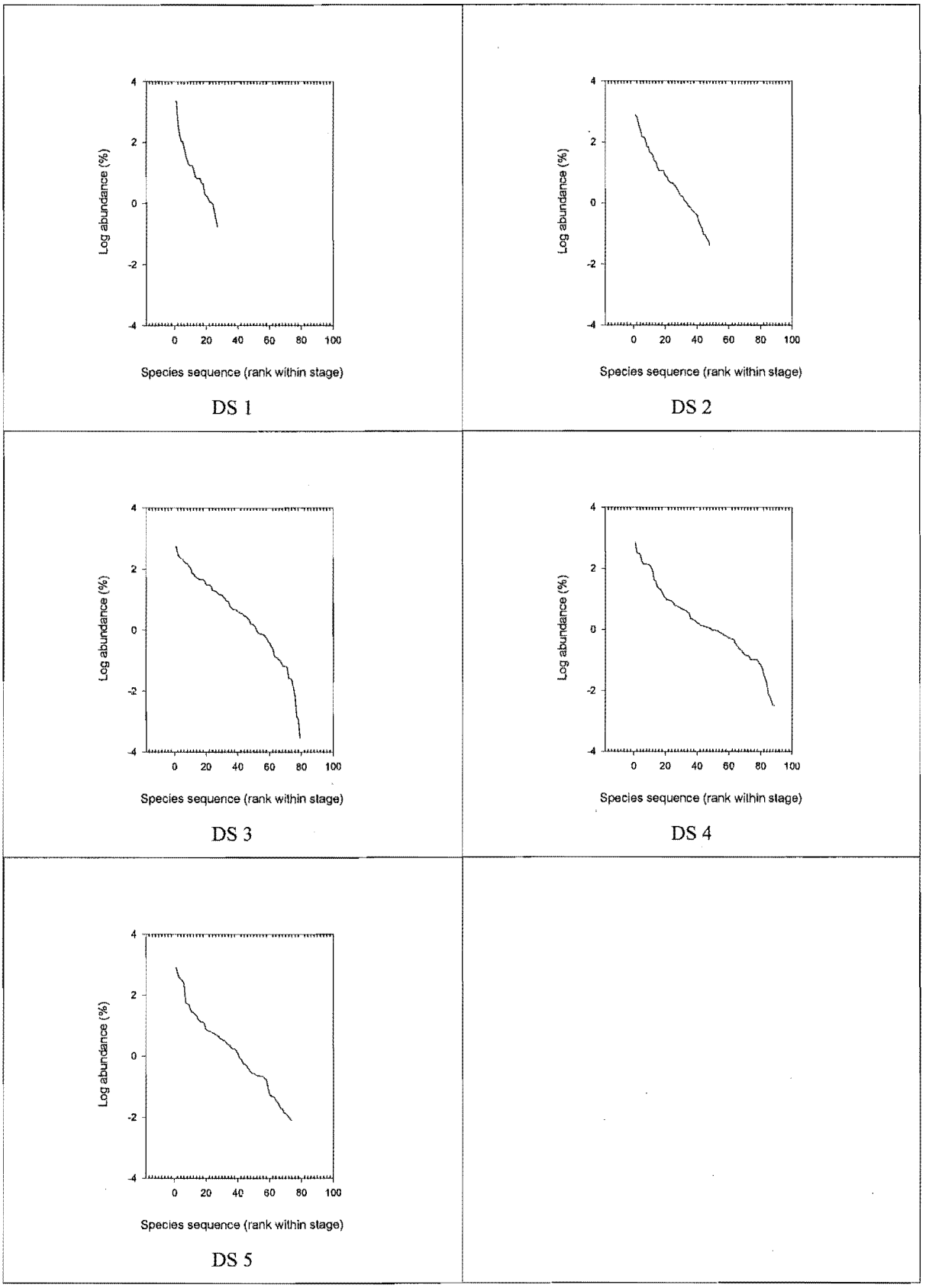

Figure 4-10 Rank/abundance plots (Log_{10} abundance versus species sequence by rank order) showing the average RAD pattern for each development stage calculated by summing the abundances for each species for all the samples within each stage.

4.4.2.6.1 Species assemblage relative abundance distributions

By using the set of graphs in Figure 4.10 to fit RAD models to each development stage by eye, the changes in the pattern of RAD with vegetation development can be interpreted. There is a gradual progression over time from a curve at DS 1 that resembles the geometric series model to something quite close to a lognormal model at DS 4, followed by a definite shift back again at DS 5 towards the geometric series model. This shift in RAD is reflected in the regression results graph for the distance from lognormal (ΔL) index (Figure 4.12) which show that the RAD tends towards a lognormal until DS 4 after which the trend reverses. The rank abundance graphs in Figure 4.10 also facilitate the interpretation in the discussion section of the trajectories observed for the two species diversity indices which are based on species proportional abundances.

4.4.2.7 Regression part two

Results are presented separately for the regressions involving the lichenometry sample set and the whole data set divided into development stages because the data points for the former are values for individual samples with precise ages and the data points for the latter are mean values for imprecise sample age class groups (i.e. development stages). Thus, by presenting the lichenometry data set separately, it is possible to gauge how much variation exists in the various facets of assemblage structure that the indices represent independent of time. With this background information in hand, it is possible to interpret the regression results for the data set where age is not accurately known with more confidence.

4.4.2.7.1 Fitting a linear model to univariate indices behaviour for the accurately aged (lichenonmetry) subset of samples

Regression statistics presented in Table 4.9 describe the properties of the relationships. Results are also presented in the form of graphs (Figure 4.11) showing the spread of the data with the fitted regression lines also included. Regression lines are only shown for significant regressions.

The indices which have significant regressions (Fpr results) were related to age, at least for the early part of the succession that these samples represent. These included: importance score, species density, DCA axis one and Simpson's diversity. The former three of these indices had a more consistent response to age than the last one (r^2 results) and all trends were positive (slope results). The index among those for which the

regression was non-significant that appears to be most related to age is functional richness; results show an almost significant positive slope. The remainder of the indices do not show any discernable trend within the relatively short time span of the lichenometrically aged samples sub-set.

Index	Linear regression results							
	SS	RMS	Fpr	r^2	Slope	Slope SE	t_{41}	tpr
Sample importance score (m^3_{cover})	0.604	0.016	<0.001	50.8	0.018	0.003	6.43_{38}	<0.001
Species density (n per $25m^2$)	1393	33.970	<0.001	28.5	0.559	0.133	4.21	<0.001
Simpson's diversity (-lnD)	10.27	0.251	0.002	19.9	0.039	0.011	3.38	0.002
Simpson's evenness ($E_{1/D}$)	0.599	0.015	0.821	*				
Distance from lognormal (ΔL)	8.190	0.200	0.167	2.3	-0.014	0.010	-1.41_{40}	0.167
Shannon's growth form diversity (H')	4.304	0.105	0.105	4	0.012	0.007	1.66	0.105
Functional richness ($\%_{site\ trait\ range}$)	4.846	0.118	0.07	0.10	0.005	0.002	2.19_{34}	0.07
Functional evenness (FRO)	0.386	0.009	0.217	1.3	-0.003	0.002	-1.25	0.217
Functional difference (V)	106.9	2.607	0.69	*				
Taxonomic diversity (Δ*)	775.5	18.910	0.598	*				
DCA axis one (S.D.)	14.06	0.343	<0.001	48	0.084	0.013	6.31	<0.001

Table 4-9 ANOVA results for testing the significance of linear regressions fitting observed data for univariate indices with lichenometry ages for each sample. * denotes that the variance of the regression residuals exceeded that of the indices value about the mean, therefore no regression slope was able to be estimated. Refer to Table 3.8 caption for an explanation of column headings. See footnote 8, p.134 for an explanation of why different indices had various n or df.

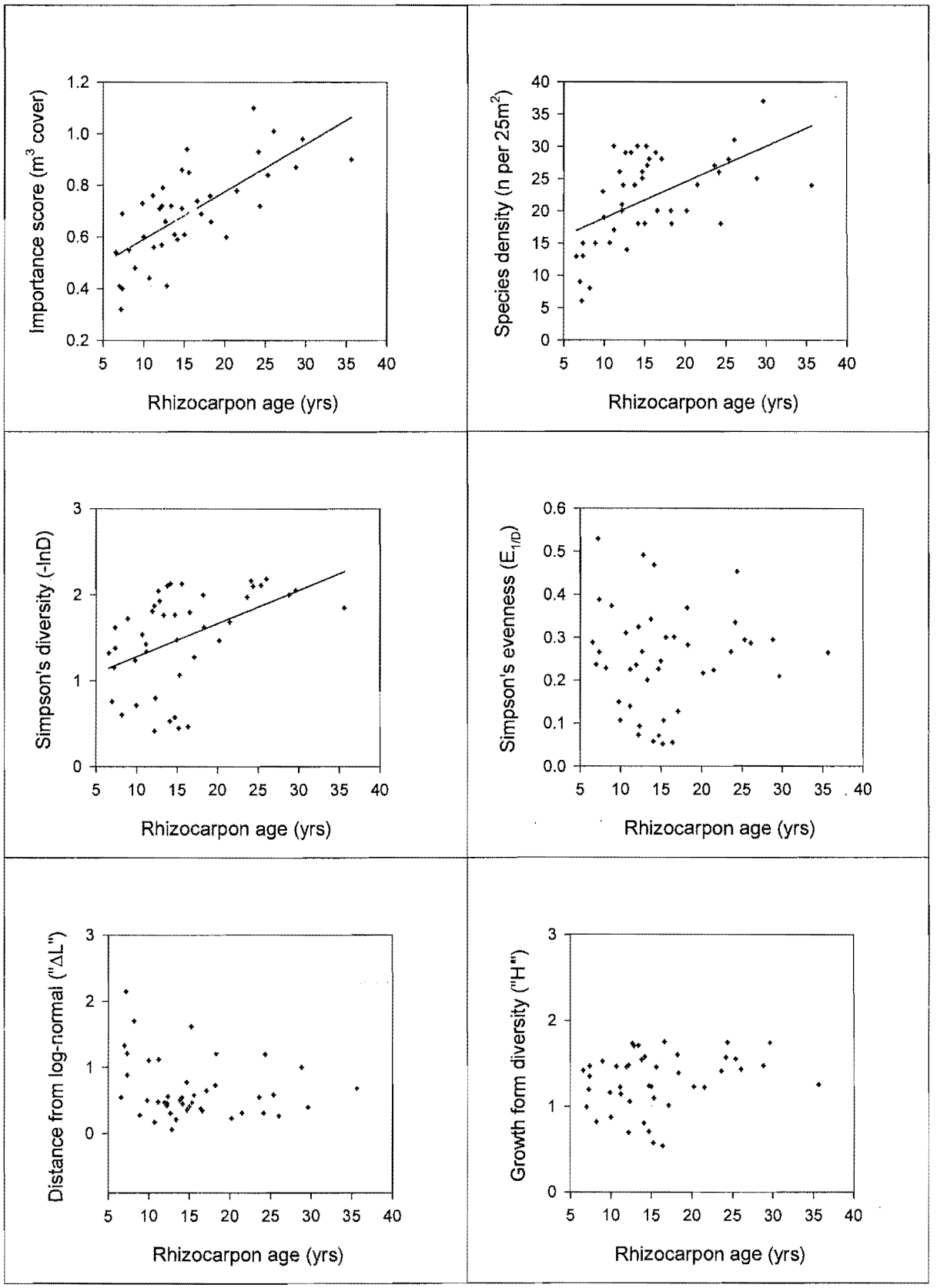

Figure 4-11 (continued on next page) Fitted regression lines and scatter plots of observed values within the lichenometry aged sub-set of plots. n=43 for all univariate indices, except importance score where n=40 and distance from lognormal where n=42. Note, fitted lines are only shown if the regression and slope parameters were significant; refer to Table 4.9 for regression statistics.

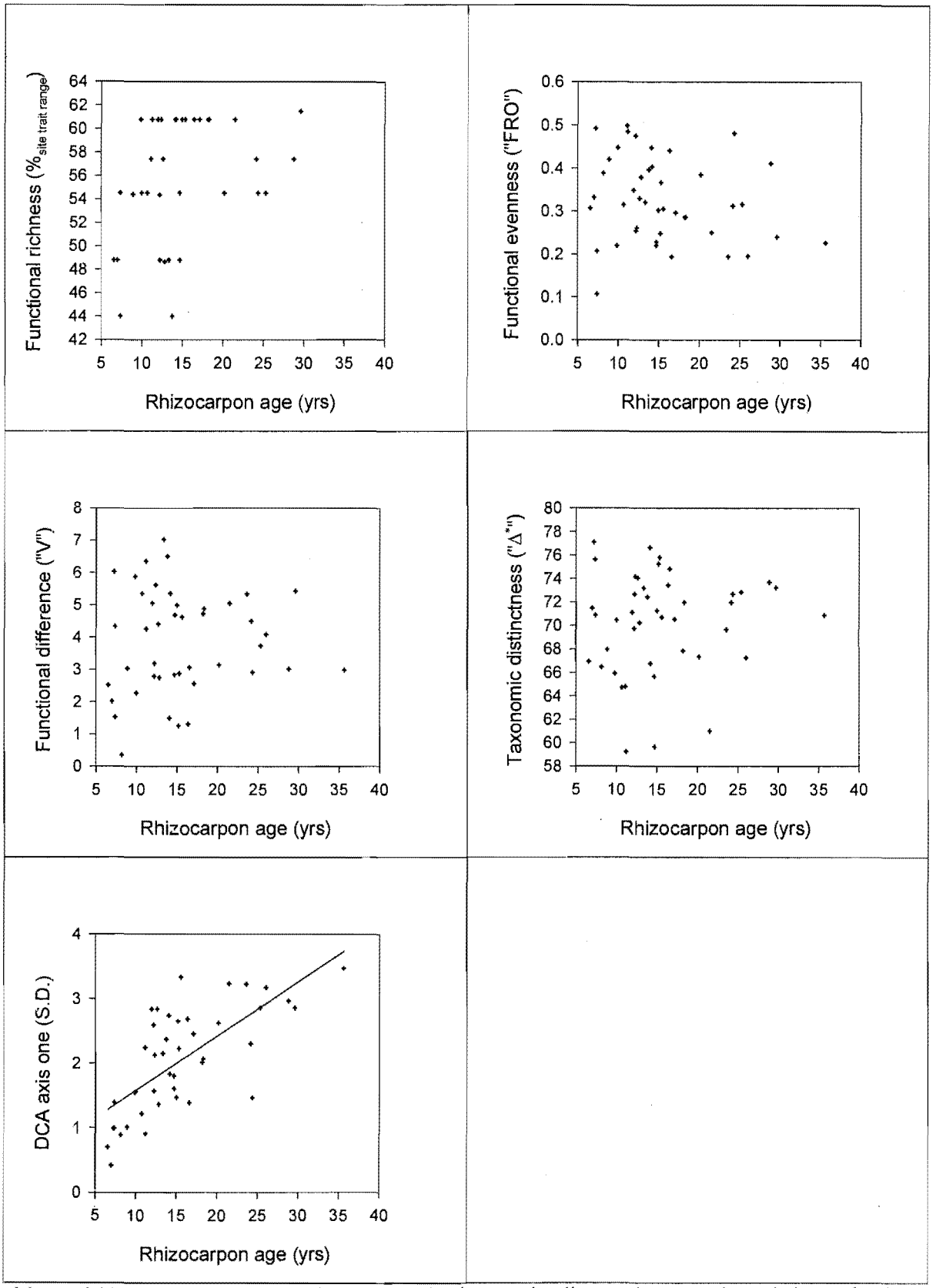

Figure 4.11 (continued from previous page) Fitted regression lines and scatter plots of observed values within the lichenometry aged sub-set of plots for all univariate indices. n=43 for all indices except functional richness where n=36. Note, fitted lines are only shown where the regression and slope parameter are significant; refer to Table 4.9 for regression statistics.

4.4.2.7.2 Fitting linear and polynomial models to univariate indices variation among development stages

This section describes the results for two sets of regressions (using linear and polynomial models) that examine the responses of indices to the whole vegetation development sequence. Owing to the ages used in these regressions for each stage being estimates of the median age of samples with variable, and in some cases unknown, individual ages, the regression statistics can not be deemed precise. Nonetheless, the significance and variance explained results are robust and valid because the effect, if any, of the age variation of samples within each stage would be to increase the intra-group variance and thereby mask any inter-group effect of age. Thus, as a whole, these results are proposed to be suitable for their intended purpose of examining index response patterns because they will only expose the stronger patterns. A significant regression (Fpr results) indicates a trend exists. The percentage variance explained (r^2) is a measure of the strength of the relationship (Zar 1999) between the pattern that the fitted values of the model indicate and reality. In order to interpret the regression significance results they need to be examined in combination with the information summarised in the graphs of Figure 4.12; particularly the within stage variation, approximate slope, trend direction and trajectory regularity. Therefore, the primary value of the results presented in Tables 4.10, 4.11 & 4.12 is as a means to improve the interpretation of the fitted and observed results graphs in Figure 4.12 rather than as an end in themselves.

Linear regression results								
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{143**}**	**tpr**
Importance score (m^3_{cover})*	4.71	0.03	<0.001	93.1	0.81	0.02	43.55_{139}	<0.001
Species density (n per $25m^2$)	5503	38.49	<0.001	81.4	12.89	0.51	23.13	<0.001
Simpson's diversity (-lnD)	31.64	0.22	<0.001	47.9	0.51	0.04	11.54	<0.001
Simpson's evenness ($E_{1/D}$)	1.51	0.01	<0.001	12.3	-0.05	0.01	-4.60	<0.001
Distance from lognormal (ΔL)	41.37	0.29	<0.001	8.3	-0.23	0.06	-3.75	<0.001
Shannon's growth form div. (H')	16.46	0.12	<0.001	16.5	0.20	0.04	5.43	<0.001
Functional richness ($\%_{site\ trait\ range}$)	24.34	0.18	<0.001	55.3	0.68	0.05	12.9_{133}	<0.001
Functional evenness (Fro)	2.32	0.02	<0.001	33	-0.13	0.02	-8.49	<0.001
Functional diversity (V)	416.6	2.91	0.023	2.9	-0.33	0.14	-2.30	0.023
Taxonomic distinctness (Δ*)	4337	31.20	<0.001	51.1	-8.26	0.68	-12.13_{139}	<0.001
DCA axis one (S.D.)	36.4	0.03	<0.001	95.4	2.26	0.04	54.86	<0.001

Table 4-10 ANOVA results for testing the significance of linear regressions of univariate indices with development stage. '*' (if after the brackets) denotes that the variable was transformed prior to regression analysis. '**' denotes that 143 was the common degrees of freedom for the regression except for indices where outliers were taken out, in which case the df is annotated as a subscript to the t value for the index concerned. Refer to Table 3.8 caption for an explanation of column headings.

Polynomial regression results								
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{142**}**	**tpr**
Importance score (m^3_{cover})*	3.39	0.02	<0.001	95	0.22	0.03	7.32_{138}	<0.001
Species density (n per $25m^2$)	4052	28.54	<0.001	86.2	-7.34	1.03	-7.13	<0.001
Simpson's diversity (-lnD)	23.94	0.17	<0.001	60.3	-0.55	0.08	-6.76	<0.001
Simpson's evenness ($E_{1/D}$)	1.47	0.01	<0.001	14	0.04	0.02	1.98	0.05
Distance from lognormal (ΔL)	34.7	0.24	<0.001	22.5	0.47	0.09	5.23	<0.001
Shannon's growth form div. (H')	10.23	0.07	<0.001	47.7	-0.05	0.06	-9.30	<0.001
Functional richness ($\%_{site\ trait\ range}$)	23.67	0.18	<0.001	56.2	-0.17	0.09	-1.93_{132}	0.056
Functional evenness (FRO)	2.28	0.16	<0.001	33.6	0.04	0.03	1.52	0.13
Functional difference (V)	189.3	1.33	<0.001	55.6	-2.68	0.21	-13.05	<0.001
Taxonomic distinctness (Δ*)	3977	28.82	<0.001	54.8	-3.96	1.12	-3.54_{138}	<0.001
DCA axis one (S.D.)	34.5	0.24	<0.001	95.6	0.26	0.09	2.80	0.006

Table 4-11 ANOVA results for testing the significance of linear regressions of univariate indices with development stage. '*' denotes that the variable was transformed prior to regression analysis. '**' denotes that 142 was the common degrees of freedom for the regression except for indices where outliers were taken out, in which case the df is annotated as a subscript to the t value for the index concerned. Refer to Table 3.8 caption for an explanation of column headings.

The 'Fpr' results in Table 4.10 & Table 4.11 indicate that all indices have significant linear and polynomial relationships with age respectively. Results of the F-test in Table 4.12 show that the polynomial model fits significantly better than the linear model for all indices except Simpson's evenness, functional richness and functional evenness for which the reverse is true. However, as can be seen from the graphs in Figure 4.10 the better polynomial fit does not imply a high degree of curvature to the relationship.

The four indices that had significant regressions for the lichenometry samples data set (importance score, species density, Simpson's diversity and DCA axis one) have among the strongest and most consistent responses to age over the whole development sequence as indicated by their slopes and coefficients of determination (r^2) from the linear regression results (Table 4.9). Of the indices with non significant lichenometry regressions which did nonetheless show a trend (slope data) albeit insignificant, every one had significant trends over the whole development gradient. However, the absence of a trend over the early part of the vegetation development did not necessarily imply that the index would be insensitive to the whole gradient (e.g. taxonomic distinctness).

Index	F statistic	Fpr	Best fit model?
Importance score (m^3_{cover})	53.60	<0.001	polynomial
Species density (n per $25m^2$)	50.84	<0.001	polynomial
Simpson's diversity (-lnD)	45.67	<0.001	polynomial
Simpson's evenness ($E_{1/D}$)	3.86	0.051	linear
Distance from lognormal (ΔL)	27.29	<0.001	polynomial
Shannon's growth form diversity (H')	86.46	<0.001	polynomial
Functional richness ($\%_{site\ trait\ range}$)	3.74	0.057	linear
Functional evenness (FRO)	0.23	0.632	linear
Functional difference (V)	170.52	<0.001	polynomial
Taxonomic distinctness (Δ*)	12.49	<0.001	polynomial
DCA axis one (S.D.)	7.82	0.006	linear

Table 4-12 Results of the F-test for the null hypothesis that the polynomial regression does not fit the data better than the linear regression. Rejection of the hypothesis ($p \leq 0.05$) means that the polynomial model predicts the observed index pattern significantly better than the linear model.

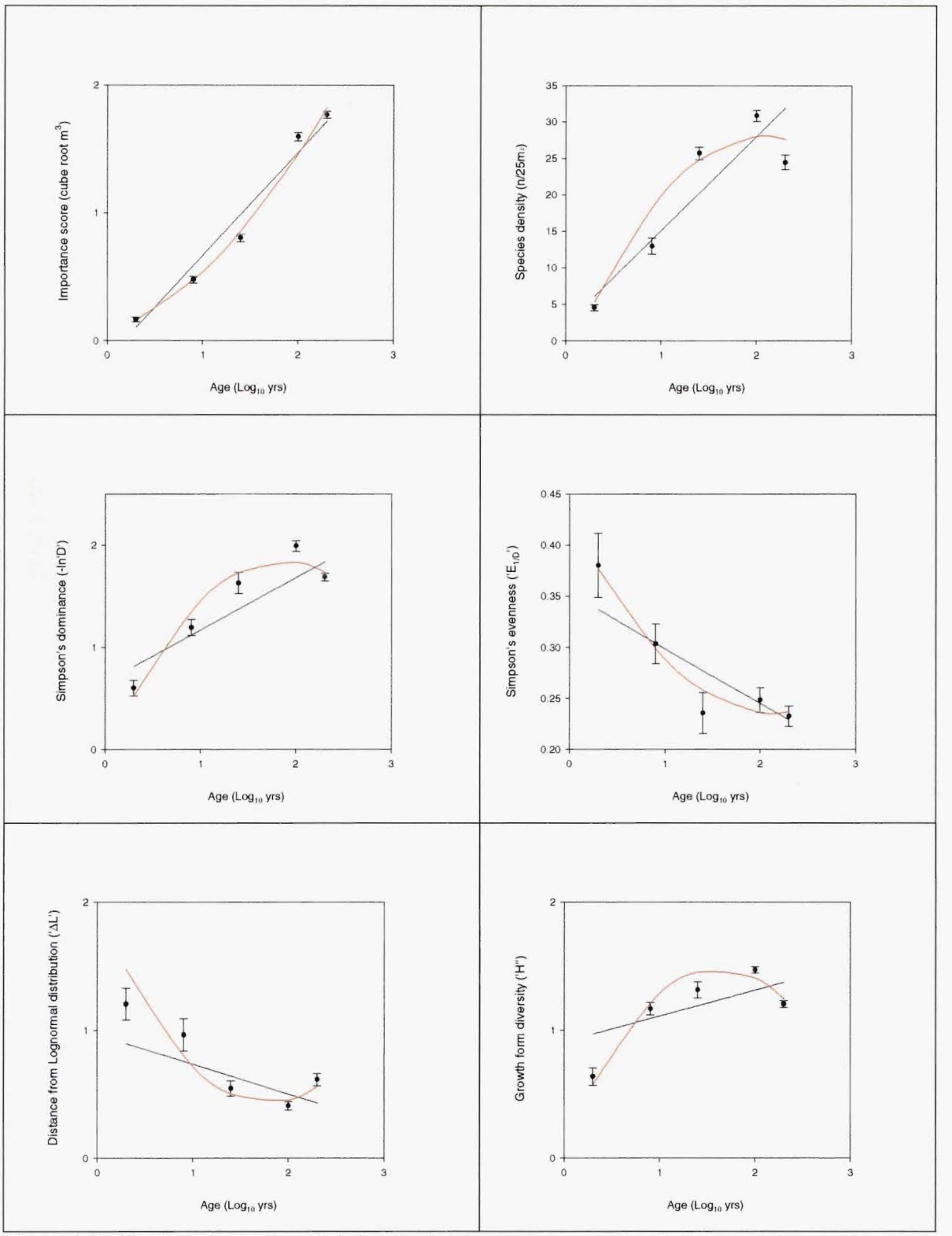

Figure 4.12 (Continued on next page) Graphs showing the mean and standard error of the mean per stage for the observed data of each univariate index, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for each significant regression, regardless of whether the slope parameter was significant, or, in the case of the polynomial model whether it was a significantly better fit than the linear model.

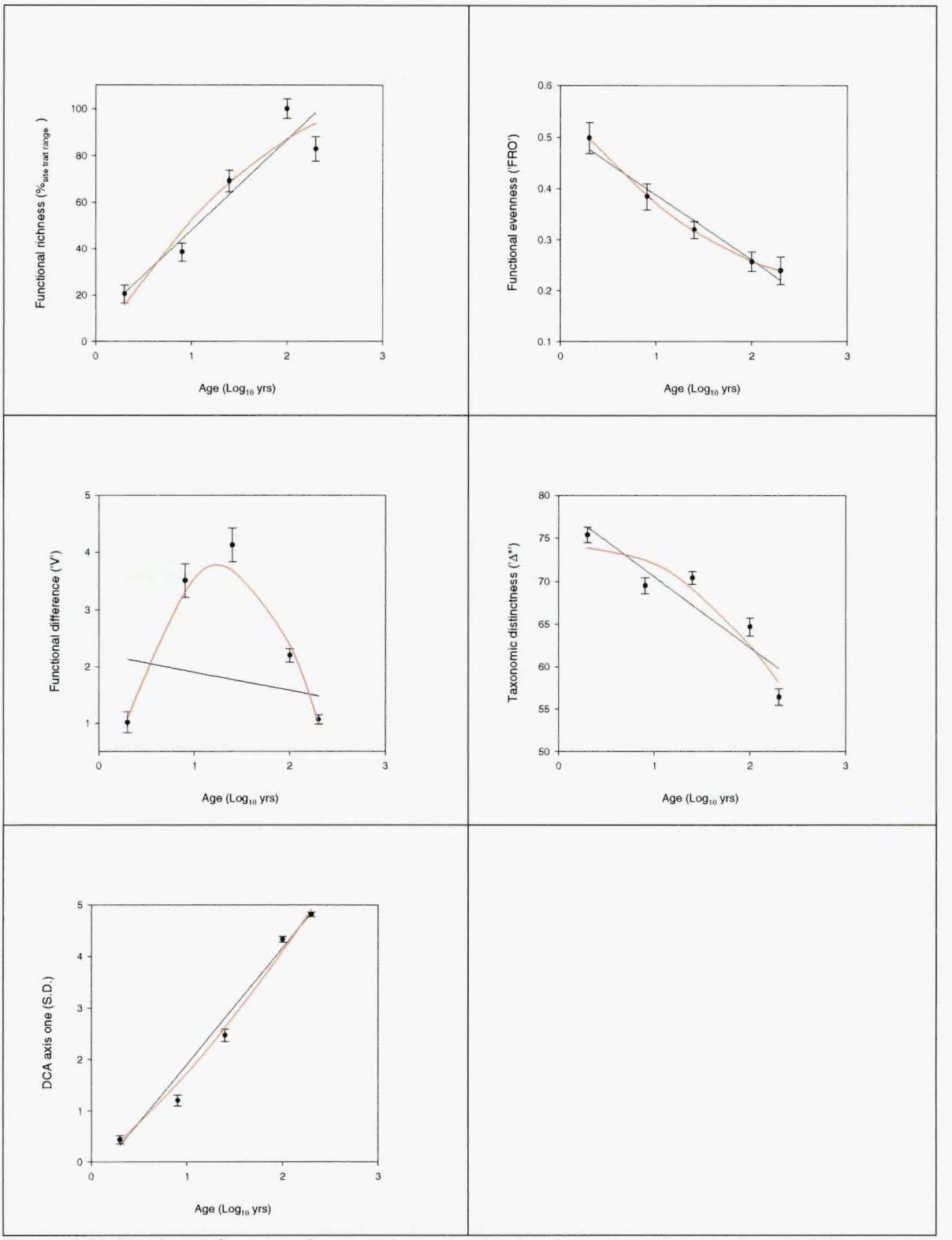

Figure 4.12 (continued from previous page) Graphs showing the mean and standard error of the mean per stage for the observed data of each univariate index, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for each significant regression, regardless of whether the slope parameter was significant, or, in the case of the polynomial model whether it was a significantly better fit than the linear model.

The patterns of index responses to the vegetation development gradient sampled in the Godley illustrated in Figure 4.12 are described in detail in the following sections, however they are summarised here into three categories:

1. Strong response and clear trend with a very consistent and smooth trajectory (either fitting a linear or polynomial model).
   - Importance score and DCA axis one

2. Strong response and clear trend with a consistent trajectory (either fitting a linear model, or, a polynomial model with limited curvature)
   - Species density, Simpson's diversity, distance from lognormal, growth form diversity, and taxonomic distinctness.

3. Clearly sensitive to vegetation development but with and inconsistent trajectory and thus no clear trend (possibly fitting a polynomial model with high curvature)
   - Functional difference

Importance score

Importance score responds strongly to vegetation development with a very consistent trajectory. The trajectory pattern is an exponential increase between DS 1 & 4 which levels off between DS 4 & 5. The pattern has a close fit to a polynomial model of low curvature.

Species density

Species density has a strong response with an increasing trend. The pattern is consistent at first with an almost linear increase between DS 1 & 4 but then it drops sharply between DS 4 & 5. The trajectory fits a polynomial model well.

Simpsons's diversity

Simpsons's diversity responds strongly to vegetation development with an increasing trend. It follows the same pattern as species density and the trajectory fits a polynomial model reasonably well.

Simpson's evenness

Simpson's evenness responds strongly to vegetation development, displaying a decreasing trend. The trajectory decreases sharply from DS 1 to 3 and then levels off. The trajectory possibly increases slightly at the end but the error bars are too large to be certain.

The trajectory fits a polynomial model but high levels of intra stage variation causes a weak fit.

Distance from the lognormal species abundance distribution

Distance from the lognormal distribution of species abundances responds to vegetation development with a clear decreasing trend. The pattern shows a consistent decrease until DS 4 after which it increases again. The trajectory fits a polynomial model quite weakly.

Shannon growth form diversity

Growth form diversity responds to vegetation development with an increasing trend. The pattern is inconsistent with an increase from DS 1 to DS4 followed by a decrease again to DS 5. The most marked change over the entire development sequence is the jump from DS 1 to DS 2. The trajectory broadly fits a polynomial model.

Functional richness

Functional richness responds strongly, with an increasing trend. The pattern is inconsistent with an increase from DS 1 to DS 4 followed by a decrease to DS 5, however the trajectory more closely fits a linear model.

Functional evenness

Functional evenness responds strongly to the vegetation development gradient. The trajectory is a smooth and consistent slightly levelling decrease, however high intra stage variation levels mean it does not fit the linear model as well as it would appear from the graph in Figure 4.12.

Functional difference

Functional difference responds strongly but very inconsistently to vegetation development. There is a slight decreasing trend overall but the trajectory is highly curved. No other index shares this pattern.

Taxonomic distinctness

Taxonomic distinctness responds strongly with a decreasing trend. The pattern is slightly inconsistent but fits a polynomial reasonably well.

DCA axis one

DCA axis one responds very strongly to vegetation development. The trajectory is smooth, consistent and linear.

4.4.2.8 Ordination - PCA

4.4.2.8.1 PCA of univariate indices

The graph in Figure 4.13 illustrates the separation of samples using the combined set of indices values and the overlaid bi-plot arrows indicate the contribution of each index to this separation. The development stages are reasonably well grouped although some overlap occurs between each stage and the next. The samples within each stage are

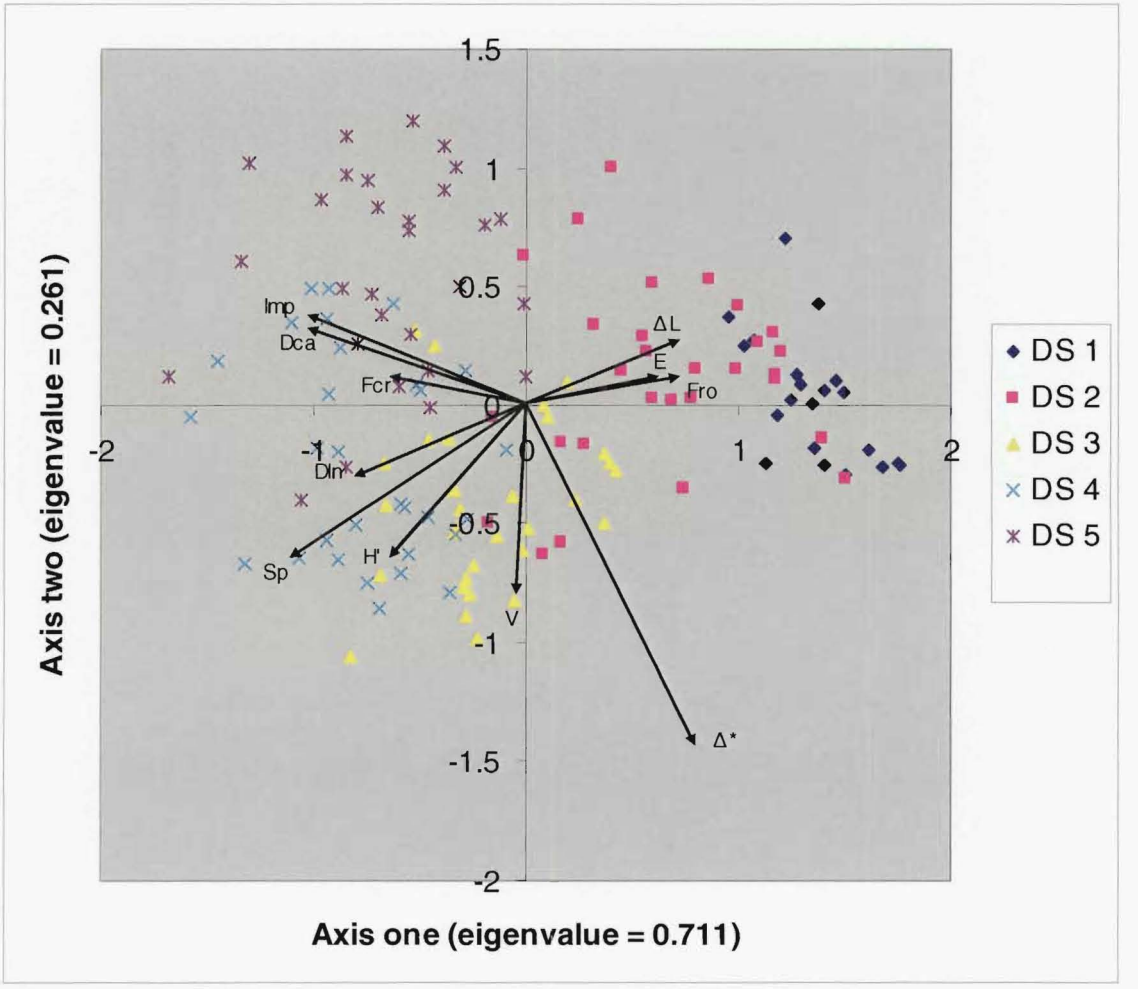

Figure 4.13 Ordination diagram of all samples based on a PCA analysis of univariate indices values. Axes one and two (shown) together comprise 97.2 % of the variation. The eigenvalues for axes one to four are 0.771, 0.261, 0.016 and 0.007 respectively. Biplot arrows directions denote the relationship of each index to the separation of the samples, arrow length is proportional to the strength of the index's contribution to the sample variation. Key to arrows codes clockwise from the positive end of axis two: ΔL=Distance from lognormal distribution, E = Simpson's evenness, Fro = Functional evenness, Δ*= taxonomic distinctness, V = functional difference, H' = Shannon growth form diversity, Sp = Species density, Dln = Simpson's diversity, Fcr = Functional richness, Dca = DCA axis one, Imp = importance score.

probably more separated overall compared to the DCA ordination that uses the complete species abundance data set. This indicates that the range of univariate indices encompass a high proportion of the variation contained within the species abundance data set. Thus, they are a good summary of the structural changes that occur in the assemblages along the development gradient. Amongst the indices bi-plot arrows there are two clear clusters, each containing three indices: in the top-left quadrant; importance score, DCA axis one and functional richness, and, in the top-right quadrant; distance from lognormal, Simpson's evenness and functional evenness. The remaining five indices are quite evenly spread and so can be thought of as representing different aspects of variation from each other. However, complementarity or otherwise of the indices' contribution toward PCA sample variation is not related to the similarity of their ecological meaning.

4.4.2.8.2 PCA of species abundance data

The object of this analysis was to assess the trajectory of vegetation development. Accordingly Figure 4.14 depicts the coordinates of the first three PCA axes for each development stage, thereby representing the trajectory of plant assemblage change in three dimensions. Most of the variation is encompassed within the first two axes (75.3 %), however the third axis does encompass a significant amount of information (8.7 % variation). The graph is orientated so as to emphasise the change in coordinates on the first two most important axes.

The points of DS 1 and DS 2 are superimposed onto one another. The trajectory can be seen to move in a highly linear fashion from DS 1 until DS 3 after which it changes direction and moves almost linearly until DS 5 with a slight deflection at DS 4. It appears from these results that the trajectory of vegetation development inferred at the Godley field site is simple with no evidence of cyclic or retrogressive behaviour.

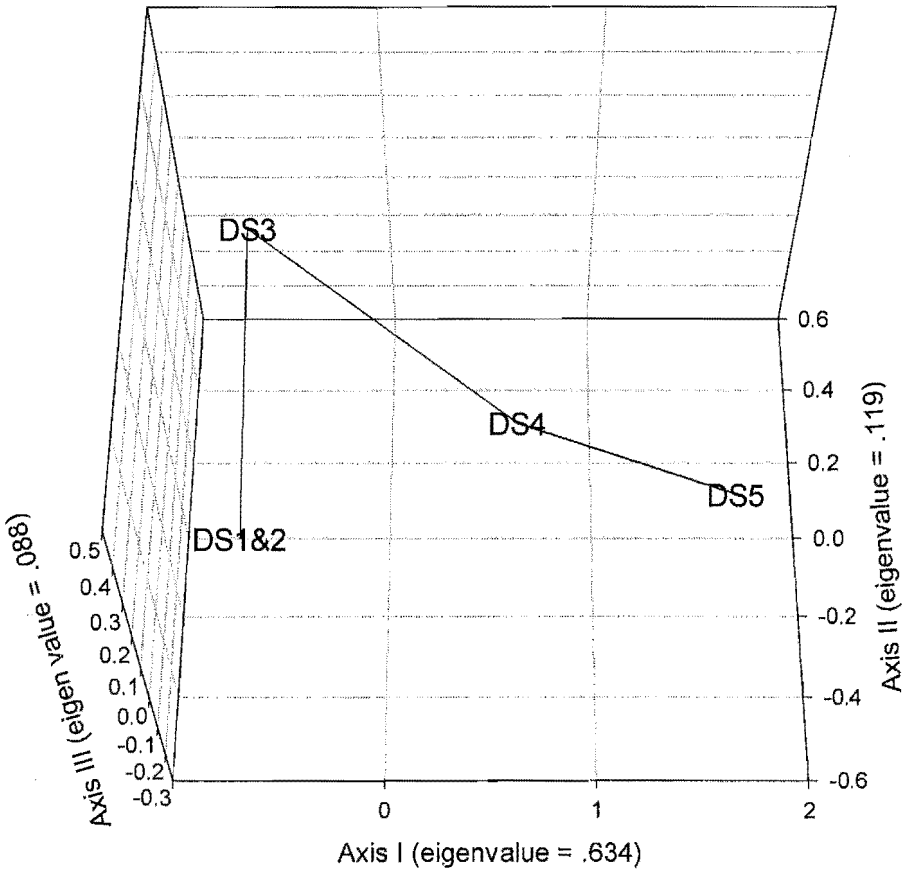

Figure 4-14 Three dimensional depiction of the vegetation development trajectory as summarised by a PCA analysis of the species abundance data.

4.5 DISCUSSION

The main objective of this chapter was to examine the response of the indices to the inferred vegetation development trajectory at the Godley Valley study site. In order to address this objective, this discussion draws upon the results to focus on the following questions.

- Has the chronosequence method accurately inferred the vegetation development sequence that would occur under the conditions of this case?
- Can index performance & pattern of behaviour be explained by either or all of:
    - Reference to successional models and general vegetation dynamics concepts
    - Comparison to other studies of succession to herbaceous communities after river flooding disturbance
    - Comparison with patterns of other indices from this study site

4.5.1 QUALITY OF CHRONOSEQUNCE INFERENCE

Results clearly show that the sampling methods used at this study site have inferred the general pattern of vegetation development that would occur on any surface throughout the study area. DCA ordination distinguished fairly discrete development stages and confirmed that age correlates most closely with floristic variation. DCCA ordination indicated that the environmental variables of most importance had been measured and stepwise regression indicated that none of these were strongly correlated with the main floristic gradients. PCA ordination illustrated that despite the number of surfaces sampled, each possibly formed by a different disturbance event, the vast majority of the variation in floristics among these could be resolved into a simple trajectory. All indications point to a largely deterministic succession, presumably as the result of a limited species pool combined with filtering effects of harsh establishment conditions and fairly predictable gradients of change in environmental conditions.

Even though all results point to a robust inference of vegetation development, there are several aspects of the sampling that do not satisfy the conditions of a chronosequence *sensu stricto*. Foremost must be the lack of opportunity to derive an accurate age for each sample. Nevertheless, lichenometry techniques at least enabled the correlation of development stages with age classes to be confirmed. Also, the similarities between the lichen-age based regressions and the five-stage based regression is very encouraging in this respect.

Assuming that most, if not all, development stages do include a random distribution of sample ages within the bounds of development stage definitions, such a range would have undoubtedly produced confounding variation about mean indices values per stage. Yet, patterns among development stages remained strong for most indices. Furthermore, these patterns are consistent with those inferred by the lichenometry aged section of the chronosequence that had an accurately estimated age gradient.

Another possible criticism of the validity of the chronosequence method in this case is the spatial extent of the study site. Distance will have introduced some variation in many aspects of environmental conditions among samples, for example, climate, disturbance regime, species invasion probabilities etc. However, on the other hand, the extensive sampling design is a strength because it enabled truer replication of the chronosequence than was possible in the other two study sites, or than is usually the case in chronosequence studies (Pickett 1989; Fastie 1990). In this case, the development stage replicates were true

chronosequence replicates in the sense that they were not simply parts of the same surface formed by one disturbance event. The large proportion of recently formed surfaces within the contemporary river bed of the study site enabled insight into the likely range of initial conditions that the chronosequence replicates from the multitude of disturbance events would have experienced. All the evidence suggests very similar conditions. Thus, the study provides a more robust application of the chronosequence experimental design by testing multiple unique examples of recovery from disturbance.

It is possible that some surfaces have been subject to post-formational flooding disturbance that was intense enough to arrest or alter the vegetation development trajectory. These effects would compromise the inferences made by the chronosequence. Evidence was found of such disturbances affecting three samples in development stage three. Their lichenometry ages were not consistent with the presence of advanced woody shrub vegetation. It appeared that a flood had exposed fresh surfaces for lichen growth but had not been intense enough to remove deeper rooted woody vegetation. It is thought that such medium intensity flood damage is rare, with lower intensity floods causing deposition, or higher intensity floods causing complete destruction of surfaces being more common. Indeed, variation in soft sediment depth (by means of differences in the surface formation event, through subsequent flooding or by differential aeolian deposition via microtopography or plant growth) was the only measured environmental variable shown to have a significant effect on vegetation development. However, the effect was not highly significant.

In conclusion, despite the complexities of this chronosequence, it has inferred a reasonably long vegetation development gradient with a simple trajectory that provides a good contrast to the other two study sites and is considered suitable to test indices response against.

4.5.2 EXPLANATION OF INDEX BEHAVIOUR

4.5.2.1 Which model(s) of succession from the literature fit the pattern in the Godley study site?

The facilitation model (Connell & Slayter 1977) describes the inferred succession in the Godley River bed well. The newly formed river bed provides harsh conditions for the establishment and growth of species characteristic of later parts of the succession (e.g. tussock grass species: *Poa colensoi*, *Festuca novae-zelandiae*). There is a distinct group of species (e.g. *Racomitrium* sp. & *Raoulia* spp.) that are able to colonise very soon after a

surface is formed that ameliorate these conditions such that they are more favourable for the growth of later successional species. This is a clear case of facilitation being the key mechanism by which vegetation development is able to proceed, but multiple mechanisms play a part in species replacements throughout the development gradient. The species compositions of each development stage (see Appendix seven) show three main groups of species in terms of their arrival time and persistence along the development gradient. There are those that establish early and do not persist into later stages, those that establish early and persist the whole way through and those that establish later on. Therefore, there is no evidence for the mass persistence of species suggested by the Initial Floristic Composition model (Egler 1954). Neither is there support for the phased arrival and replacement of species cohorts described by the Relay Floristics (Egler 1954) model, although the emphasis this model places on the mechanism of facilitation is valid. The 'facilitation model' proposed by Connell & Slayter (1977) implies a more gradual invasion of later-succession species. However, adoption of the facilitation model to explain succession in the Godley does not suggest that other mechanisms are not active (e.g. inhibition), simply that facilitation is the dominant mechanism of successional change. Nor does it deny the importance of processes such as competition and gradients of resource availability, but describing succession in terms of net responses to the relative importance of processes (e.g. (Walker & Chapin 1987) requires a great deal more information than is available for this study.

The successional process typical of upland braided river beds in the region of the study site has been well described by previous authors (Cockayne 1911; Calder 1961; Burrows 1977) so only a brief summary is given here. Early colonist species improve site conditions by trapping wind-blown sediment, stabilising the substrate as well as increasing organic matter and nutrients. The increase in sediment provides more favourable water availability and establishment sites. A wide range of creeping, tuft forming and tussock forming species invade the new sites. A diverse species assemblage with a range of strategies (*sensu* Grime 2001) co-exists for some time, however, eventually the early successional species disappear through inhibition (i.e. competitive suppression, *sensu* Tilman (1985)) by the more vigorous grass species. Plants such as matagouri and the introduced legumes (*Trifolium* spp.) improve soil fertility by fixing nitrogen (Burrows 1977), further encouraging dominance by the grasses. When grasses become dominant, their cover is so dense that matagouri is unable to continue germinating (Dobson & Burrows 1977) and many other low growing species are confined to inter-tussock spaces

(e.g. *Coprosma* spp., *Muehlenbeckia axillaris* etc.). Evidence from studies investigating the regeneration of other native woody species in similar grassland environments suggest that the exotic grass species (e.g. *Agrostis capillaris*) are particularly important suppressors (Rogers 1996; Widyatmoko & Norton 1997). Previous authors describing succession in the study site region, do not comment on models, but their observations and comments support the adoption of the facilitation model for this study site.

The two international studies described in the introduction as being suitable comparisons to the study site (Bliss & Cantlon 1957; Viereck 1966) were published previously to Connell and Slayter's seminal 1977 paper that described the facilitation model. Nevertheless, the descriptions of the successional sequences they inferred appear to fit the facilitation model closely. Indeed, their explanation of successional process relied on the concept of allogenic (plant-mediated) change. Thus, in both cases a 'facilitation' mechanism identical to that occurring in the study site was described. In common with the study site, the foremost facilitation event involved specialist herbaceous colonists that improved site conditions to provide greater establishment opportunities, primarily by accumulated fines and organic matter.

4.5.2.2 Discussion of index behaviour by comparison with other information from this study site and other similar study sites

There are no opportunities for interpretation of the indices response patterns in the Godley by comparison to other studies except for importance score and species density. This is because previous studies of braided river bed vegetation development sequences were of a descriptive nature with no statistical analysis of the composition or structure of assemblages having been conducted.

Therefore, indices response patterns are interpreted by cross-referencing between the different analyses performed on the Godley assemblages as well as referring to the change in species composition among the assemblages.

4.5.2.2.1 Importance score

The increase in importance score with increasing age of primary successions is a well documented phenomenon. Asymptotic patterns of above ground biomass increase have been reported as typical for grassland successions specifically (Gleeson & Tilman 1990), albeit from a secondary succession example. In longer term successions, decreasing rates of biomass increase are associated with declines in productivity toward the latter stages of succession owing to resources being more fully utilised (Burrows 1990; Peet

1992; Vitousek 2004). This resource limitation could be an explanation for biomass stabilisation over the longer term in the Godley, however no soil nutrient data is available to confirm this. Certainly, similarity of the floristics and physiognomy of DS 5 with a terrace community in the Waimakariri thought to be 1,000 years old (Burrows 1977) indicates that the importance score trajectory measured in the Godley would tend to reach a plateau beyond the maximum age sampled. Vierrek (1966) inferred that plant cover increase followed the same pattern in the Muldrow Glacier outwash floodplain vegetation development as in the Godley. Bliss & Cantlon (1957) also found a similar pattern for plant cover in the Colville river floodplain development sequence. However, after around 2,000 years the Colville system underwent a retrogression associated with deteriorating soil conditions that resulted in a decrease in cover from a previously stable plateau. It is possible that the Godley system could undergo a similar retrogression but floodplain dynamics preclude the possibility of surfaces persisting for long enough to allow advanced soil impoverishment to take place.

4.5.2.2.2 Species density

The pattern of species density can be easily explained. The phase of rising species numbers would have corresponded with a period of increasing diversity and density of establishment sites, as well as a probable increase in fertility as was observed by Burrows (1977) in the Cass floodplain. The decline of species density at the end of the vegetation development probably resulted from a rise in the rate of species extinctions to above that for immigration, owing to the dominance of competitively superior grasses (especially exotic species) and invasive ground layer herbs. Interpolation from species lists provided by Singleton (1975) from the five development stages she studied in the Waimakariri floodplain show that the response pattern of species density was the same there as was found in this study. Furthermore, the same competitively superior species became common at the same point along the vegetation development gradient.

4.5.2.2.3 Indices related to proportional species abundances

Simpson's diversity followed the same pattern as species density did in the Godley, albeit with a shallower slope. The decreasing trend of Simpson's evenness with time explains why diversity did not increase at the same rate as species numbers. Comparison of the pattern of Simpson's evenness with the change in shape of the RADs shows that a decrease in evenness cannot be simply interpreted as few species dominating the plant

abundance, at least among the low levels of evenness that occurred along the entire development gradient. This is because Simpson's evenness takes into account what proportion of the total species density those dominant species comprise. Closer examination of the RAD patterns shows that although fewer species comprise the majority of plant abundance in stage one than stage five, the evenness is lower in stage five because the dominant species there represent a smaller proportion of the total species assemblage. RAD graphs can also be used to interpret the pattern of distance from the lognormal distribution of species abundances. The tendency towards the lognormal during the first four stages is associated with an increasing number of the species having medium proportional abundances. The pattern reversal that occurred at the final stage was due to a massive loss of rare species. Species density values indicated that this loss of rare species was not ameliorated much by immigration, allowing the loss to precipitate a large effect on the species RAD. No information on species proportional abundances for other gradients of herbaceous vegetation development on braided river beds is available.

4.5.2.2.4 Functional diversity indices

Growth form diversity follows a similar pattern to both species density and Simpson's diversity, but different processes governed the richness and proportional abundances of growth forms than for species. Examination of the species list shows the richness of growth forms would have reached a maximum early on in the development sequence, thereafter increases of growth form diversity would have been associated with an increase in evenness of growth form abundance. However, during the final stage the dominance of the tussock and non-tussock grass growth forms was so high that diversity decreased despite the maintenance of peak growth form richness.

In the grassland development sequence of the Godley, the functional trait of leaf area is loosely associated with growth form. For example, in general, dicotyledonous herbaceous and shrub species have smaller leaves than the grass and rush species. Therefore, the general trend of increase in functional richness results from increasing species numbers, as well as the tendency for species turnover during succession to introduce species with larger leaves. The decrease in functional richness at the end of the vegetation development is because the majority of species lost from the oldest assemblages were those with the smallest leaves. The decrease in functional evenness further emphasises the dominance of larger leaved grass species indicated by other indices. The progressive nature and extent of the dominance of native tussock and non-native sward

forming grass species is indicated by the fact that functional evenness decreases consistently despite increases in the range of the leaf area trait (i.e. functional richness) throughout most of the sequence. The pattern of functional difference shows that despite the decrease in evenness of abundance in functional trait space, the dispersion of abundance in functional trait space increases, at least until the assemblage of DS 3. This is probably due to the as yet incomplete vegetative cover of DS 3 allowing the co-existence of the earlier assemblages characterised by plants with small leaf areas with the assemblages of the mature stages characterised by larger leaves. In later stages, the loss of species with small leaf areas and dominance by species within a small part of the range in leaf area acted to reduce functional difference.

4.5.2.2.5 Taxonomic distinctness

The consistent decreasing trend of taxonomic distinctness whilst functional richness and species density both increased is at first counter-intuitive. The explanation for species density is that as it increased, the diversity of taxonomic levels higher than species did not increase accordingly; i.e. many of the immigrating species were closely related. The explanation for functional richness is that the leaf area character tends to vary at the genus level rather than at the species level for the taxa represented in this study site. Thus, taxonomic distinctness measures a different aspect of variation within the species data to the other indices, as is also clear from the PCA analysis of sample separation based on indices values (Figure 4.13). Research on the behaviour of the index by its creators (Clarke & Warwick 1998; Warwick & Clarke 1998a) suggests it typically varies differently from indices based on species data that take no account of taxonomic relationship, but, the decreasing trend observed in this study site contradicts their claim that it responds positively to succession.

4.5.2.2.6 DCA axis one and the development trajectory in general

DCA axis one indicates relative amounts of species turnover among stages as the vegetation development proceeds; it illustrates the vegetation development gradient itself that is perhaps the most basic process of plant succession. The greatest amount of species turnover is between DS 3 & DS 4. In fact, this interval represents almost half the length of the gradient. Different facets of the shift in assemblage structure that accompanies the large amount of change occurring at this point in the development sequence were picked up by several of the indices discussed above. Depictions of the development trajectory by both

the DCA and PCA analyses represented this change as a trajectory deflection. It is postulated that the two parts of the trajectory represent different phases of the succession, whereby assemblages dominated by colonist species with a high degree of spatial variation are replaced by a far more homogenous assemblage of late successional species. The decline in species turnover between the final stages, despite this section of the gradient representing the longest time interval, shows that rates of change were slower at this time than at any other during the succession. This late decline is interpreted as an increase in stability of the plant assemblages associated with the end of primary succession.

Many indices picked up a marked shift in assemblage structure between the final two stages. The PCA analysis of species abundances also reflected this, displaying a second deflection of the trajectory. It is postulated that this second deflection was owing to the sharp increase in the abundance of exotic species. New Zealand alluvial grasslands are particularly vulnerable to introduced species adapted to disturbed and nutrient rich conditions (Walker & Lee 2002). It is probable that without the effect of invasive species, the indices responses would have just levelled off rather than shown a reversal of previous trends.

4.6 CONCLUSION

In summary, the chronosequence sampled at the Godley Valley provides a good inference of the general pattern of vegetation development during succession in this environment. In addition, the study provides the most detailed account known of to date that describes the plant assemblages occurring along the primary succession gradient typical of braided rivers in New Zealand. Most of the indices responded strongly to vegetation development with a clear trend. The differences in the species identity and assemblage structure of the Godley site compared with the other two forested sites enables more enlightened conclusions to be made about which indices are more suited to the evaluation of restoration success, as discussed in the final chapter.

5 FOREST REGENERATION AFTER GLACIAL RECESSION IN THE FOX VALLEY, WESTLAND

5.1 OVERVIEW

In this chapter, the study site in the Fox Valley, South Island, New Zealand, and reasons for its selection are described. General methods are detailed in Chapter two; only methods specific to the Fox study site are described fully in this chapter.

The vascular plant assemblages and environmental characteristics of six development stages, ranging in age from six to approximately 5,000 years were analysed. The development stages sampled were chosen so as to be approximately evenly spread over the vegetation development gradient in terms of species turnover rather than time. This spacing aims not only to optimise the accuracy of the vegetation development trajectory inference but also to maximise the floristic differences among stages so that indices response can be resolved over and above the heterogeneity within each stage.

The development gradient at the Fox site is long with a simple trajectory, indicating deterministic assembly. The majority of indices have a strong and consistent response to vegetation development. The discussion covers the quality of the chronosequence sampled and seeks to explain the indices response behaviour with reference all the results herein and to international studies of vegetation development on de-glaciated terrain.

5.2 INTRODUCTION

5.2.1 PREVIOUS SUCCESSIONAL STUDIES ON DE-GLACIATED TERRAIN

Worldwide studies interpreting vegetation patterns on recently de-glaciated terrain constitute an important source of information on primary succession (Matthews 1992). Over the last 40 years in particular these studies have made important empirical and theoretical contributions to understanding the ecology of succession (Matthews 1999). Studies have taken place mostly in North America (e.g. Glacier Bay, Alaska, USA; Klutlan Glacier, Yukon, Canada; Robson Glacier, B.C., Canada; Mt Rainier, Washington State, USA.) and Europe (e.g. Nigardsbreen and Storbreen, Norway; Grand Glacier d'Aletsch, Switzerland) with notable exceptions in 'ice-free' Antarctica and New Zealand (primarily the Franz-Josef Glacier) as well as less detailed investigations in South America (Burrows 1990; Matthews 1992, 1999).

Early successional studies on de-glaciated terrain concentrated on description and mapping of the vegetation. These have been followed by more detailed research on the soil changes that accompany vegetation change and on the mechanisms for vegetation change. More recent research developments include the ordination of communities, autoecological studies and the identification of successional trajectories (Matthews 1999). The studies at Glacier Bay, Alaska (Cooper 1923; Crocker & Major 1955; Reiners et al. 1971; Bormann & Sidle 1990; Fastie 1990; Chapin et al. 1994; Walker 1995) provide one of the best known examples of a vegetation chronosequence (Burrows 1990), where up to eight development stages spanning 1,500 years have been described in detail (Reiners et al. 1971).

In New Zealand, the retreat of the two valley glaciers at Fox and Franz Josef provide a reasonably well dated vegetation sequence that is able to infer the development trajectory of the last 14,000 years (Wardle 1980b). The Franz Josef has been the most studied sequence of the two, probably because of better accessibility and the greater area of intermediate aged surfaces available. Several studies have attempted to age the Franz Josef sequence (Stevens 1968; Wardle 1973; Burrows 1990; Almond et al. 2001), resulting in the oldest surface now being dated at >120,000 years. Nonetheless, with the exception of Wardle's study of primary succession (1980b), studies at Franz Josef have concentrated on soil development (Stevens 1968; Stevens & Walker 1970; Richardson et al. 2004). The vegetation descriptions of these latter studies have been relatively brief, although the trajectories given by Richardson et al. (2004) have added to the knowledge of vegetation development patterns.

The Fox Valley Glacier has received far less attention with the most significant publication (Wardle 1973) summarising historical records as well as Wardles' own survey information on glacial movements. The most recent publication pertaining to vegetation development at the Fox (Wardle 1980b) classifies the community types of some of the plant assemblages present, but refers to point analysis descriptions carried out in the Waiho valley below Franz Josef Glacier for species composition details. Thus, until this study no detailed vegetation analysis had ever taken place in the Fox Valley (B. Watson, Dr. P. Wardle pers. comms. 2004) despite the existence of baseline data on surface age and distribution as well as the opportunity it presents for making a comparison to the well known Franz Josef chronosequence.

5.2.2 VALLEY GLACIAL PROCESSES LEADING TO THE FORMATION OF LANDFORMS AS SURFACES FOR VEGETATION DEVELOPMENT

Valley glaciers exhibit distinct processes from glaciers on gentler terrain typical of colder regions of the world (Knight 1999). Valley glaciers take the form of ice tongues projecting into steep sided valleys from snow accumulation areas (névés) higher up. The mass and dimensions of a glacier depend primarily on the balance between accumulation and 'ablation' (melting, sublimation and wind erosion) in the névé, and are therefore dependent on climate (Knight 1999). Owing to annual or seasonal climatic variations, the position of the glacier terminus is rarely stationary and movement rates are rarely constant (Matthews 1992). Nevertheless, within the same region glaciers tend to respond in a broadly similar way to climatic trends (Knight 1999). Distance from the terminus of a retreating glacier is directly related to terrain age, but unfortunately in a non-linear way; necessitating further information to obtain numerical age estimates of de-glaciated terrain (Matthews 1992).

Glaciers worldwide have retreated, except for small intermittent advances, since the Little Ice Age (~200-400 yr BP) with rates being accelerated in the 20th century (Burrows 1990; Walker & del Moral 2003). This has provided excellent opportunities for studying vegetation development in 'recently de-glaciated terrain'; collectively known as the 'glacial foreland'.

A glacier carries rock fragments within its ice or on its surface ranging in size from silt to huge boulders. Sediments in glacier forelands fall into two classes; those deposited by glacier ice (tills) and those deposited subsequently by glacio-fluvial or tributary activity (outwash alluvium) (Whiteman 1995).

5.2.3 FACTORS OTHER THAN TIME AFFECTING VEGETATION DEVELOPMENT IN RECENTLY DE-GLACIATED VALLEY TERRAIN

Although the physical landscape in the glacial foreland has a limited range of landforms and sediments, it would be an oversimplification to regard glacier foreland ecosystems as explicable solely as a function of terrain age (Matthews 1992). In addition to age, variation in texture, topography and fertility of the substrates influences initial conditions for plant colonisation and soil development, and also therefore, the vegetation succession that follows (Burrows 1990). However, owing to post-formational modification by processes such as consolidation, stabilisation, frost-weathering and aeolian deposition, surface roughness has been shown to decline rapidly after de-glaciation (Matthews 1992).

Thus, by the time substrates are stable enough to support plant colonisation, the substrate textural variation may typically be less pronounced than it would appear from studying substrate profiles.

The study of glacial foreland terrain formation has shown that the 'terrain age' (determined as the timing of cessation of formation activity) of a surface is less than the time since exposure from the ice and may even be considerably less than that of a neighbouring moraine crest. This difference in age is owing to the continuation of deposition by glacial meltwater and run-off streams, substrate consolidation, sub-surface flow, frost action, aeolian erosion & deposition (Matthews 1992). Thus, the definition of surface age for this study, referred to hereafter simply as 'age', pertains to that of Matthew's terrain age. The point of zero age theoretically corresponds to the time when conditions for plant colonisation to proceed existed. It is likely that small differences in age exist even between adjacent parts of the same surface owing to uneven rates of glacial recession and spatial variability of post-formational processes. Owing to these variables, surface ageing information was obtained from the immediate locality of the vegetation samples.

Gross differences in initial disturbance type can have lasting effects upon successional trajectory, primarily by influencing surface substrate characteristics and soil formation processes (Birks 1980; Wardle 1980b). Therefore, a chronosequence *sensu stricto* must occur across a similar substrate type.

Secondary disturbances occur on a lesser temporal and spatial scale than primary disturbances, contributing, along with random variation, to the 'ecological-noise' (inexplicable variance) within each development stage. Secondary disturbance types of importance to the glacial foreland environment include landslides, snow damage, flood related damage/sediment deposition, aeolian deposition of loess, aeolian erosion/desiccation/cooling, frost damage and grazing (Matthews 1992, 1999). Personal observations at Fox suggest that important secondary disturbances are likely to be tree-fall and flooding.

The momentum created by the initial disturbance continues to drive system development in deglaciated terrain for long periods (White & Jentsch 2001), even though system structure is governed by successional processes and somewhat stochastic species assembly (Young et al. 2001). Generally, during later development stages in such environments, secondary external disturbances and the physical environment have less effect on plant assemblages than biotic interactions and internal disturbances (e.g. tree

senescence) (Burrows 1990; Matthews 1992). This would suggest floristic convergence, however, there is debate in the literature about whether successional trajectories on glacier forelands are convergent or divergent (Vetaas 1994; Caccianiga et al. 2001; Kaufmann & Raffl 2002) and how much trajectories are dependent on secondary disturbance (Matthews 1999). The existence of convergence in de-glaciated terrain successions in New Zealand is backed up by observations made in this study, by Wardle (1980b), and by Richardson et al. (2004). Indeed, Richardson et al. (2004) suggest that a major external disturbance (e.g. a high magnitude flood) would be required to change the trajectory during later development stages.

This chapter considers a temperate vegetation development sequence that began on new glacial till and outwash alluvium of various kinds within one relatively small locality. The sequence spans approximately 5000 years of development and is reconstructed by means of sampling a chronosequence of six development stages that are distributed with a bias towards the younger end of the sequence. This time span corresponds approximately with the progressive phase of forest succession in this environment (Richardson et al. 2004), which leads to a tall and structurally diverse moist forest. The possible imperfections of the chronosequence method of studying succession in this environment, outlined in this section, are controlled for as far as possible within the sampling design. The rate of change and trajectory of the vegetation succession are discussed and comparisons are made to the findings of other authors at both the Fox and Franz Josef. Unfortunately, there is currently no opportunity for direct observation to compliment and verify the chronosequence method because previous sites of vegetation surveys in the Fox Valley were not permanently marked.

This chapter seeks to address thesis questions one and two in the context of the data from the Fox Valley chronosequence:

I. *How do floristics vary with age and does the main floristic gradient correlate more closely with age than any other environmental variable?*

II. *Are all the indices examined sensitive to vegetation development and does their response follow a consistent trajectory as recovery progresses?*

5.3 METHODS

Only those methods unique to the Fox study site are detailed here. Methods common to all three study sites are described fully in Chapter two, general methods. The methods section in this chapter follows the same structure as those of Chapters three and four.

5.3.1 STUDY SITE

5.3.1.1 Site selection criteria

The study site was chosen in preference to other possible sites for the following reasons:

- Reliable ageing of chronosequence development stages possible (baseline data and reasonably well preserved glacial landforms exist).
- Chronosequence vegetation development occurs over a minimal environmental distance.
- No previous detailed (high sampling effort) vegetation studies have been carried out in the locality but comparative baseline data exist on other successional trajectories in the region.
- Easy logistics compared to the Godley Valley & Lake Thomson sites. This facilitated collecting data on a higher number of vegetation development stages than at the other sites studied within the time available.
- Low densities and impact of invasive plants and animals.
- Provides an interesting comparison to the well studied Franz Josef Glacier chronosequence that occurs within the same general environment.

5.3.1.2 Study site description

Fox Glacier terminus is a popular tourist destination easily accessible by foot, located approximately seven km south-east of where state highway six crosses the Fox River (see Figure 5.1) in Westland/Tai Poutini National Park, South Island, New Zealand (43° 32'S., 170° 3'E.).

The Fox Valley lies in a tectonically active zone of highly folded and fractured bedrock planes, positioned between the main Alpine Fault and the Main Divide (Coates & Chinn 1992). At the main Alpine Fault, the steep sided valley ends abruptly to meet an extensive alluvial plain; the distance from here to the glacial terminus is only c. five km.

This section of the valley is hereafter termed the 'lower' valley. The lower valley is a classic steep sided U-shaped glacial valley, with peaks rising either side to c. 1800 m a.s.l. The lower valley floor is no more than 400 m wide and carries a swift, high sediment load main river fed by melt-water and numerous rain-fed tributary streams which frequently flood (Coates & Chinn 1992). The plentiful sediment, that forms the moraine debris features and fills the floor of the lower valley, is comprised of a mixture of Torlesse greywacke sandstone and various types of schist (Gair 1967; Guyon 1967).

The study site surfaces are spread throughout the lower valley, spanning a longitudinal distance of c. four km (see Figure 5.2), and varying in altitude between 275 and 225 m a.s.l.. They are situated either on the 'sandur' (Icelandic: sand plain) floodplain consisting of glacio-fluvial outwash sediments and alluvium from tributary streams, or, on kame terraces above the valley floor consisting of moraine debris and glacio-fluvial outwash.

The current climate of the study site is wet temperate. The nearest meteorological station at Franz Josef township (c. 150 m a.s.l.), c. 25 km to the north, gives a mean annual temperature (1926 – 1975) of 10.8°C, with a mean January maximum of 18.5°C and a mean July maximum of 9°C (Hessell 1982). The position of the recording station would have a roughly equal climate to the lowest sampled part of the Fox Valley (DS 6). Average annual rainfall (1999-2003) for Fox township (1.5 km N of DS 6 at 170 m a.s.l.) is 4,753 mm (courtesy Fox Alpine Guides Ltd.). Predictions for Fox township

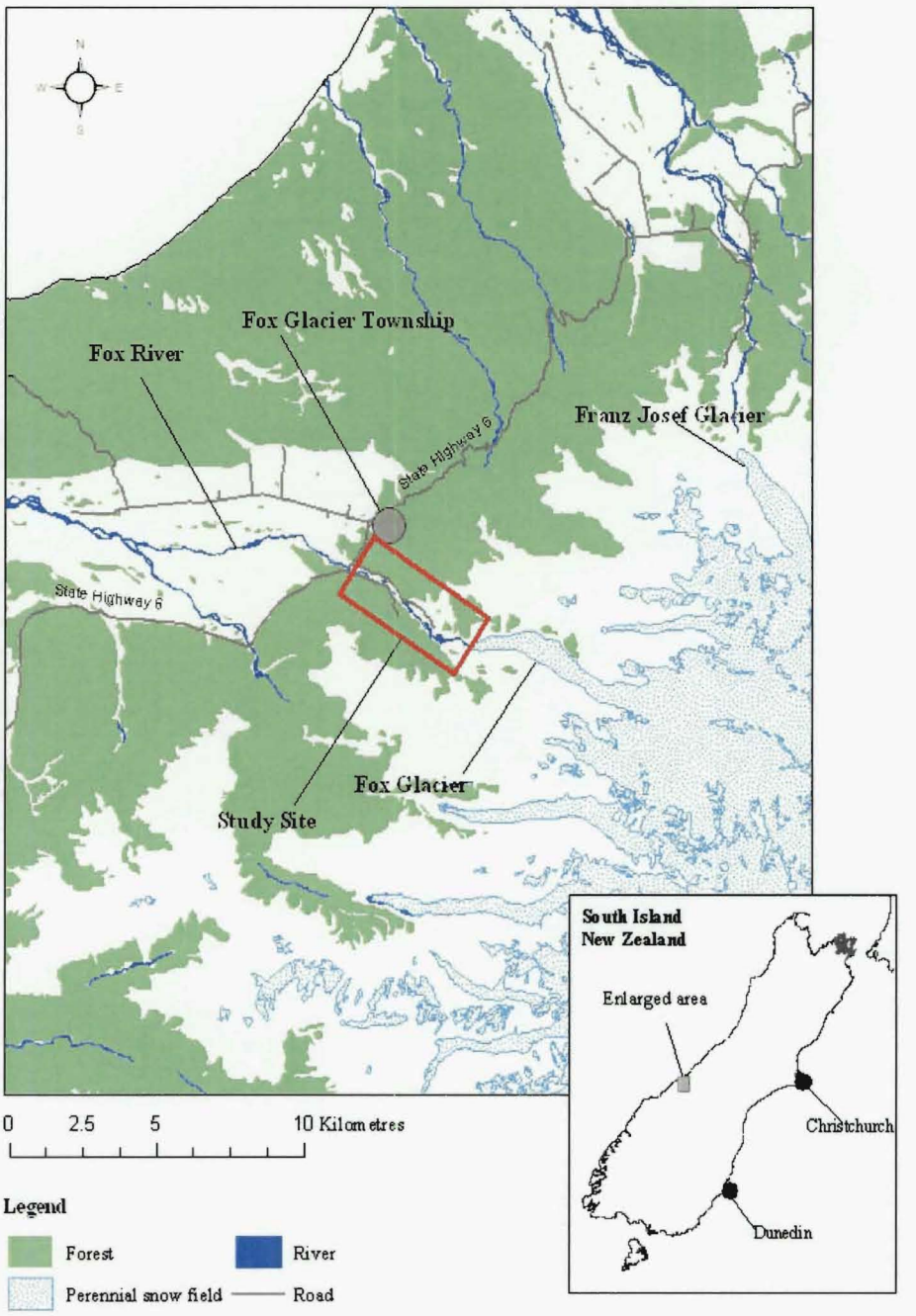

Figure 5.1 Map showing the location of the Fox Glacier study site within the South Island, New Zealand

from Isohyet maps of the region (New Zealand Meteorological Service 1973) are similar to this figure. The Isohyet maps also predict that rainfall is likely to increase, with increasing distance up the valley, to around 6,000 mm at the position of the current glacial terminus. Although no data exists for temperature, it also is likely to vary with distance up the valley as a function of increased elevation and decreased insolation, as well as from catabatic winds off the glacier itself. Thus, a rainfall and temperature gradient exists along the study site. Importantly, the climate would have been similar among surfaces during their respective initial colonisation periods because of the proximity of the glacier to all surfaces during this phase of their development.

The development of soils on glacial outwash material was studied at the Franz Josef Glacier by Stevens (1968). He found an organic layer develops rapidly and shallow weathered horizons form within 1,000 years, progressing to a rapidly leaching mature podsolic soil within 10,000 years.

The predominant vegetation type in the vicinity of the study site (on young non-podsolised soils and where the vegetation has not been subject to major disturbance) is lowland tall podocarp/broadleaved forest; this is consistent with most of central Westland at altitudes below 400 m (Wardle 1977). This is a relatively speciose and structurally complex forest type, where scattered large rimu (*Dacrydium cupressinum*) and miro (*Prumnopitys ferruginea*) are emergent over a main canopy dominated by kamahi (*Weinmannia racemosa*) and southern rata (*Metrosideros umbellata*). These forests are characterised by abundant lianas, epiphytes and tree ferns.

Previous vegetation studies in the Fox Valley have identified the vegetation types present and their species compositions (Wardle 1975, 1977, 1980a). Another study by Wardle (1973) provides the basis for the chronology of the succession taking place at Fox. A further paper (Wardle 1980b) combines previous work in the Fox Valley and other primary succession examples in Westland to describe successional pathways in more detail. The vegetation succession occurring throughout the whole of the Fox Valley appears to follow a broadly generic trajectory, characterised by several easily distinguishable plant assemblages. Early pioneer plants (e.g. *Poa* spp. and *Raoulia* spp.) provide sites for shrub species (e.g. *Olearia avicenniifolia, Carmichaelia arborea and Coriaria arborea*) to establish. These shrubs grow rapidly to form tall scrub with a dense canopy. Pioneer forest species (e.g. *Carpodetus serratus* and *Schefflera digitata*) establish under the scrub canopy and gradually emerge to form a low forest, which in turn provides

suitable conditions for the longer lived tall forest species to establish and eventually dominate. Finally, podocarps are able to establish and become common canopy emergents.

Invasive plants and animals are assumed to be at low and fairly even densities, having been controlled by DoC throughout the valley by spraying or poisoning/trapping respectively for several years. In addition, the high level of human presence in the valley would act to discourage ungulate herbivores. Thus, it is assumed that there is a low level of extrinsic ecological disturbance by invasive organisms across the whole study site.

5.3.2 FIELD METHODS

5.3.2.1 Identification of glacial landforms

The preliminary goal of fieldwork in this study site was to identify the location and boundaries of each distinct glacial landform, or, 'surface'. The sketch map produced by Wardle (1973), showing the recent chronology of glacial recession, provided a useful starting point for this exercise. However, considerable ground-truthing with the aid of aerial photos (provided by DoC Hokitika) was required to locate intact demarcating landform features such as moraines, levées and terraces. Landform boundary features were often indistinct and discontinuous, rendering the formation dates of many areas indeterminate. Homogeneity of substrate and topography aided identification of surfaces, assuming that the extent of such homogeneity indicated a formation event with similar processes acting throughout.

Table 5.1 overleaf summarises the features of the surfaces identified in this survey within the Fox Valley. As indicated in Table 5.1, all surfaces recorded by Wardle (1973) were confidently identified during this survey except for 'I'. This surface had been totally destroyed by re-working of sediments by floods and landslides. Therefore, in this survey, 'I' refers to a substituted surface of similar age but in a different location to the 'I' recorded by Wardle. Surface 'J' post-dates Wardle's survey, being in front of the terminal moraine produced by the last glacial advance in 1998.

Surface ID code	Landform description	Selected for c-seq study?	Reasons for not being selected for c-seq.	Development stage in c-seq	Estimated age (yrs)
J*	Glacial outwash surface	Y	-	1	6
I*	Tributary outwash surface	Y	-	2	30
H	Kame terrace	N	fragmentary landform	-	40
G	Glacial outwash surface	Y	-	3	73
F2	Kame terrace	N	small area	-	160
F1	Glacial outwash surface	N	small area	-	156
E	Glacial outwash surface	Y	-	4	159
D	Kame terrace	N	small area	-	169
C	Meltout / retreat debris	N	gross substrate difference cf. other surfaces	-	250
B	Glacial outwash surface	Y	-	5	400
A	Kame terrace	Y	-	6	5000

Table 5-1 Descriptions of distinct surfaces identified during this study within the Fox Valley, as well as whether and why they are used for the chronosequence. Surfaces are ordered from youngest to oldest (J to A). The surface ID codes correspond with the surfaces of the same codes detailed by Wardle (1973) except for those marked with an asterisk (I & J); see text below for explanation. 'c-seq'= chronosequence.

5.3.2.2 Criteria for choosing surfaces to sample a chronosequence

The second goal of fieldwork in the Fox study site was to decide which of the identified surfaces were suitable for sampling. To be suitable, the surface had to be a terrace landform, regardless of process of origin. It also had to have enough extent within a 50 m limit of the landform boundary to fit nine randomly located replicate plots such that each plot would have at least 10 m between it and the next plot. As it is impossible to

reconstruct the precise timing and location of historic glacial processes, it is assumed that by keeping within a small distance of an even age feature such as a kame terrace or terminal moraine, age variation within each surface is kept reasonably small and constant.

In addition, the surface micro-topography and substrate type had to be reasonably even[1] and homogenous[2] respectively, both among and within surfaces, owing to their influence on micro-site provision for seedling establishment of pioneer species (Wardle 1980b). Substrate type was not possible to measure accurately because it has been progressively obscured by soil development. Therefore, a visual assessment of substrate was made from exposed surface profiles at road cuttings, washouts or levées.

By following these criteria, six of the surfaces identified were chosen to comprise the chronosequence (see Table 5.1). These surfaces will be referred to hereafter by their development stage number from one through to six, with six being the oldest stage. Their location within the Fox Valley study site is illustrated in Figure 5.2. Annotated photographs in Figures 5.3 and 5.4 also indicate their location as well as giving an impression of their appearance.

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[1] Only minor levels of undulations or concavity or convexity were permitted.

[2] The range of substrate variation accepted was between glacio-fluvial fine sediment with total rocks covering <25 % but large rocks covering <5 %, and glacio-fluvial sediment comprised of fines, gravel and pebbles with no rocks. Size definitions for substrate classes were: large rock 200-1,000 mm ∅; small rock 50-200 mm ∅; pebbles and gravels 2-50 mm ∅; fines <2 mm ∅.

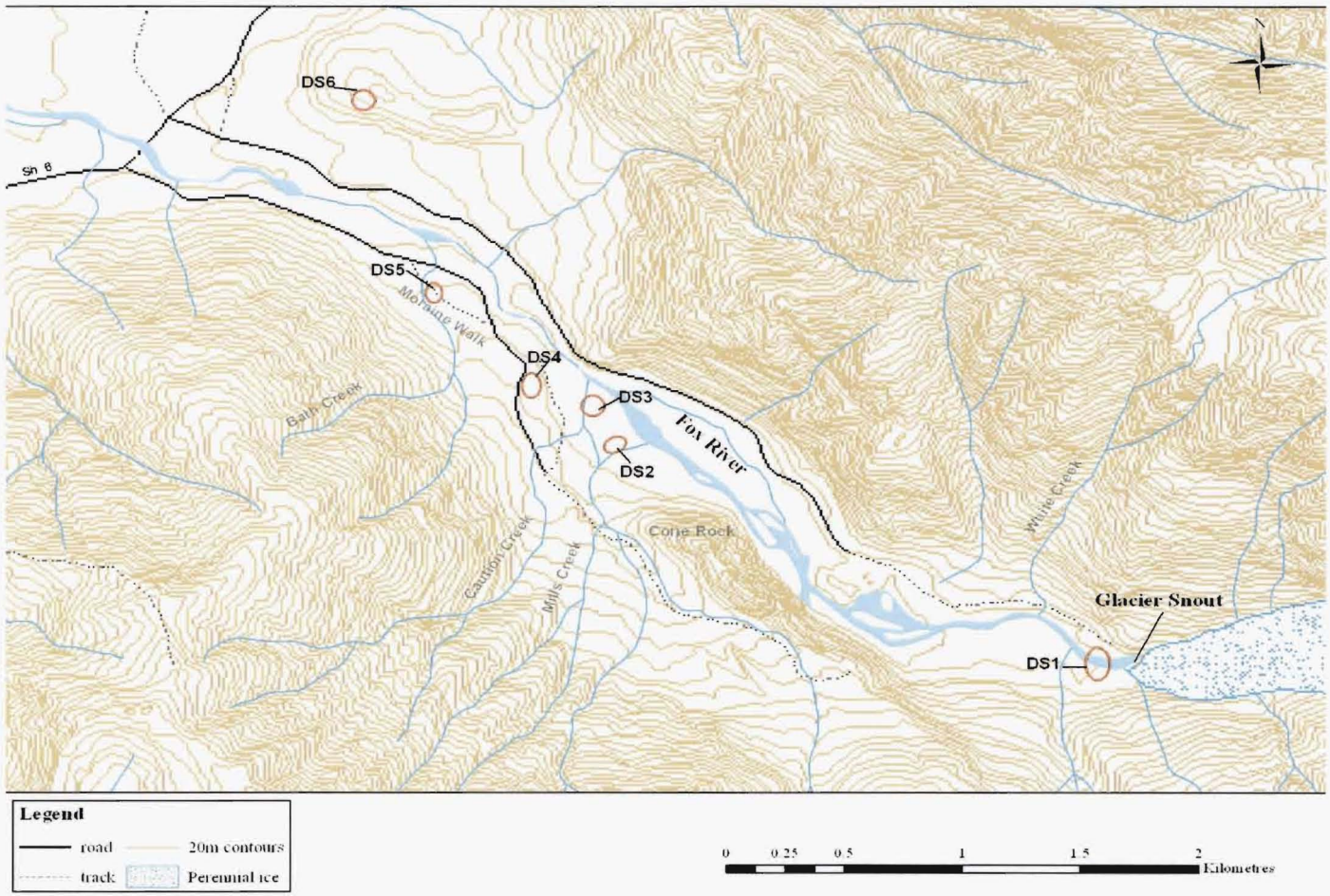

Figure 5.2 Map showing the precise location of the sampling zones for the six development stages within the Fox valley study site

Figure 5.3 View from cone rock of the lower part of the Fox valley sampling area showing locations of development stages 2, 3, 4, 5 and 6.

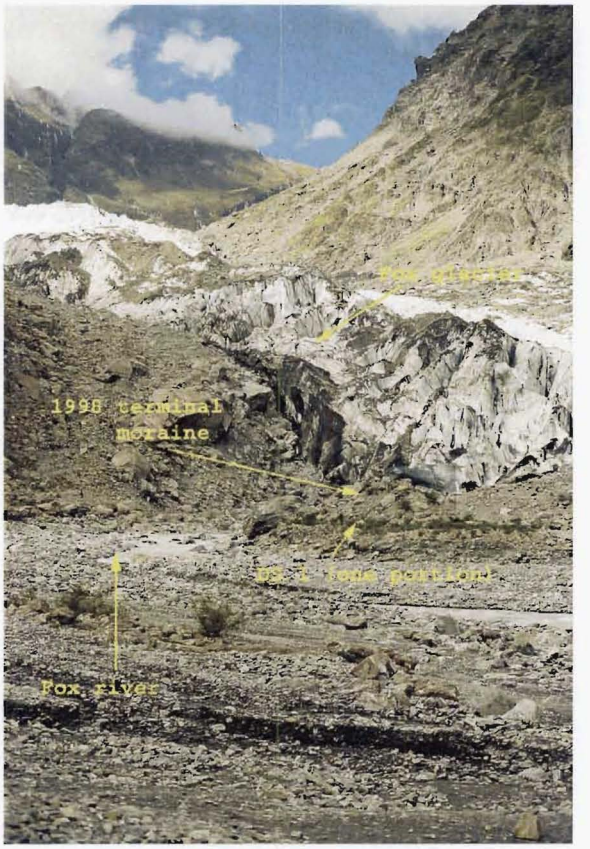

Figure 5.4 View of the upper Fox valley sampling area showing the glacier snout and DS 1.

5.3.2.2.1 Surface formation processes

To aid understanding of the surfaces upon which sampling was undertaken their formation processes, as deduced from field observations and published descriptions of glacial dynamics (Wardle 1973; Matthews 1992; Whiteman 1995; Knight 1999), are summarised as follows.

On the down-valley edge of DS 5, and on the up-valley edge of DS 1, are small crests of glacial till (terminal moraines) probably formed by push action during small advances. The substrate of DS 5 appears to have been heavily modified by glacio-fluvial deposition post retreat, whereas, DS 1 substrate has received similar modification pre and post retreat. Development stage six is on a 'kame' terrace. This was most probably formed from deposition of coarse and fine alluvium in the trench typically found between the glacier and lateral moraine ridge during glacial retreat. Development stages three and four are on terraces found at the margin of the glacio-fluvial valley 'sandur' landform. The sandur is an expanse of coarse alluvial sediments (particularly cobbles, gravels and sands) characterised by braided channels and relatively stable marginal terraces.

5.3.2.3 Sampling design

5.3.2.3.1 Plot size

10 x 10 m plots were adopted for this site for two linked reasons. Firstly, the results from the previous season's sampling at Lake Thomson show 10 x 10 m plots to be adequate for the range of vegetation types that occurred across that chronosequence from herbaceous to tall vegetation. Secondly, the range and spatial variation of species diversity among the development stages at Fox appeared to be similar to the Thomson site (with the possible exception of DS 6), judging by personal observations during reconnaissance trips.

Species accumulation curves were constructed (full methods in section 2.1.1.2) mid field-season with data from the four plots thus far sampled to confirm the 10 x 10 m plot size was suitable to sample the species diversity of all stages. These curves are not shown because the early inflexion that took place for all development stages by the third plot is clearly displayed in the species accumulation curves constructed with the complete set of samples shown in Figure 5.5. The early inflexion means that plot size was suitable to sample species diversity effectively, as discussed in section 2.1.1.2.

A nested sampling design was adopted for DS 6 in order to quantitatively test that the 10 x 10 m plot size was sufficient to sample the relative abundance distribution of the

species assemblage there, considering the large size of some individuals compared to the other stages and to the plot size; see Appendix nine for details. The 10 x 10 plot size was retained for this stage.

5.3.2.3.2 Sampling effort

It was estimated by visual extrapolation of the mid field-season species accumulation curves (constructed from four samples in each stage and not presented) that a minimum of nine[3] samples should ensure sufficient sampling effort. In fact, the accumulation curves from the full data set (Figure 5.5) provide evidence that a sample size of nine was indeed sufficient. The curves in Figure 5.5 for all development stages show an early inflexion followed by a slow increase in species observed.

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[3] Although even numbers of replicates are preferable for statistical comparisons among groups (Zar 1999), in reality dangerous access (glacial melt-water channel changing course mid-way through field season) limited the number of replicates obtainable to six for DS 1. The other five development stages had the full complement of nine replicates.

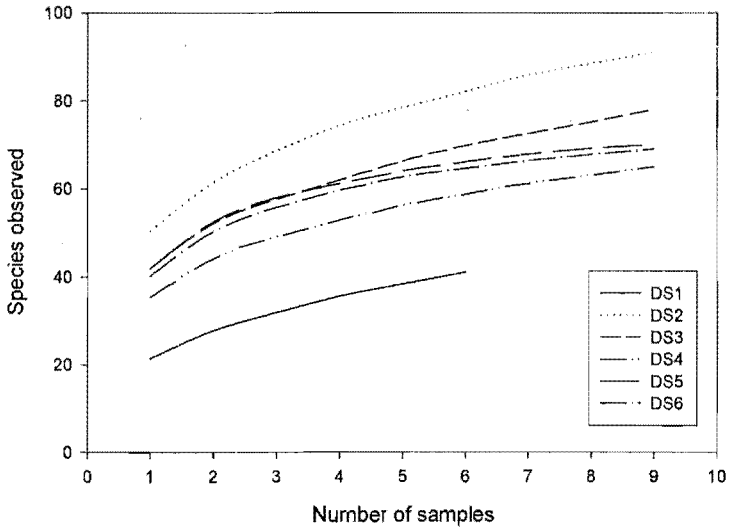

Figure 5-5 Smoothed species accumulation curves for the six sampled development stages.

Estimates of species richness (S_{max}), using methods detailed in Chapter two, provide further quantitative evidence that sampling effort was adequate to characterise the species diversity of all stages. An average of 82.1 % of S_{max} was cumulatively observed among the development stages (calculated from data in Table 5.2). This figure is high and equates to adequate sampling effort. Furthermore, the low standard error of this figure (± 1.74) shows that sampling effort was relatively even among the stages, a fact also illustrated by the parallel nature of the lines representing S_{obs} and S_{max} in Figure 5.6. This proof of even sampling effort means that comparison among stages of indices related to aspects of species diversity (see univariate indices calculation methods, Chapter two) are robust.

Development stage	S_{obs}	S_{max}	S_{max} SD	proportion of S_{max} observed (%)
1	41	54	4.79	75.9
2	91	111	3.80	82.0
3	78	98	4.83	79.6
4	65	80	2.81	81.3
5	70	80	3.47	87.5
6	69	80	2.67	86.3

Table 5-2 Results per development stage of: 'S_{obs}' observed species area accumulation data, 'S_{max}'.estimate of species richness (Jacknife 1 estimator of maximum theoretical assemblage species richness observable assuming exhaustive sampling), 'S_{max} SD' standard deviation of the species richness estimate and the proportion of S_{max} cumulatively observed.

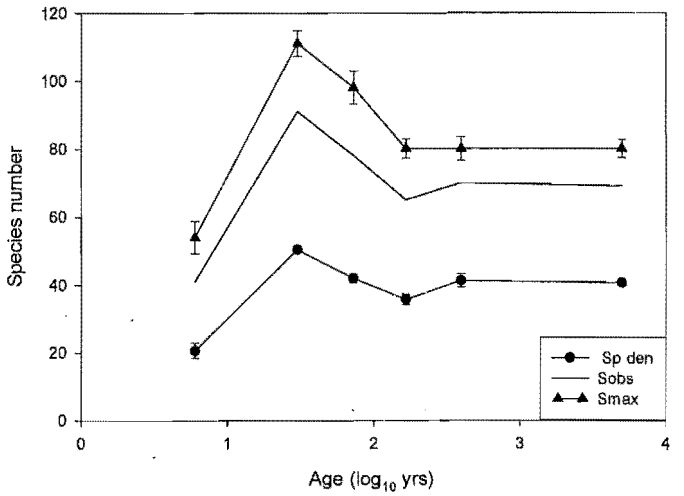

Figure 5-6 Three measures of species diversity per development stage for comparison. Sp den= mean species density (species observed per replicate sample) with standard error bars, S_{obs}= observed species richness from accumulated replicates' sample data, and S_{max}= mean estimated theoretical maximum species richness (assuming exhaustive sampling) and standard deviation bars.

Development stage six sample data provides evidence to support the accuracy of the Jacknife 1 algorithm used to estimate S_{max}. Species area accumulation figures rise to 75 with a sample size of 20 (from 69 with a sample size of nine), by including the extra 11 samples from the nested sampling design tested (see Appendix nine). Therefore, the theoretical maximum of 80 species (Smax) obtained from the Jacknife estimator (Table 5.2) would seem reasonable for an exhaustively sampled assemblage.

5.3.2.3.3 Replicate sample numbers required for statistical power

As a rough guideline, a power analysis was performed on data from the previous season's Lake Thomson site using the 'POWER' procedure in GenStat, before data collection for the Fox site was started. The Lake Thomson chronosequence was considered to be an acceptable analogue for the Fox chronosequence, based on reconnaissance trips to Fox made by myself. Reconnaissance observations focused on levels of species turnover among stages and floristic variability within stages; both were judged to be relatively similar between sites. When the power analysis was run assuming stages would have equal floristic variance to the stage with the highest floristic variation from Lake Thomson, the minimum number of replicates required was indicated to be seven. Since this number of replicates was less than that previously estimated to be required to effectively sample

species diversity at Fox, a further power analysis, using Fox mid field-season data for example, was not considered necessary.

5.3.2.3.4 Systematically stratified random sampling method

The method employed to achieve the aims of the sampling design outlined above is a 'systematically stratified random' design, *sensu* Mueller-Dombois and Ellenberg, (1974). The stratification is a systematic division of the total sampling area potentially available into approximately even aged surfaces. Implicit in the meaning of surfaces employed by this study is that they can be comprised of discontinuous areas, provided there is no reasonable doubt that the areas are of even age[4]. Randomness is incorporated by locating potential individual plot sites using random number tables to dictate compass direction and distance from random points on a surfaces' boundary. Once located, potential plots were only sampled subject to meeting selection criteria designed to reduce factors hypothesised to confound the effect of age on vegetation development. With respect to the chronosequence concept, replicate plots per surface are 'pseudoreplicates'.

5.3.2.3.5 Plot location criteria

These selection criteria were derived by reviewing field notes taken during the initial phase of fieldwork when surfaces were being identified and observationally based inferences were made about the processes behind, and influences on, vegetation development. The theories put forward by Wardle (1980b) about factors influencing the rate and direction of vegetation development in several local examples of primary succession trajectories following glacial retreat were also incorporated and agree with my own observations. The selection criteria used to decide whether to sample potential plots were consistent across all surfaces.

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[4] Even age was inferred by assessing similarity of formational origin across surface extent, and, that surface boundaries correspond with an age boundary on Wardle's (1973) map.

Firstly, each plot was sampled only if it was reasonably well drained; this was defined as there being no evidence of widespread water-logging after rain. Poor drainage is influential on local successional trajectories, and, when occurring on young soils, is an indicator of in-filled moraine trenches[5] (Wardle 1980b). Because the natural process of soil podsolisation would not be expected to have advanced to the stage where it results in widespread waterlogging within 5,000 years (D. Norton pers. comm. 2004), a time span equal to the age of the oldest surface, it was judged sufficient to avoid waterlogged areas rather than investing the time to measure drainage.

Further selection criteria were a relatively stable substrate comprised of mostly small to medium sized (<100 mm longest axis) particles, and, not obviously having been subject to gross secondary disturbances such as flooding, grazing or human activity. Vegetation mediated secondary disturbances such as tree fall were accepted because they are viewed to be integral to the process of vegetation development. Finally, the slope had to be less than five degrees from horizontal.

Variables beyond the scope of this study to measure and which are possibly also influencing the vegetation pattern are; micro-variation in original substrate and topography, seed source, major secondary disturbances occurring too soon after vegetation establishment to be observable at the time of the study, variation in primary disturbance type and intensity, and, exotic animal species presence and density. Historical accounts are too recent and piecemeal to do more than tentatively confirm the lack of importance of the latter two variables for the youngest four surfaces only.

5.3.2.3.6 Plot demarcation

If the immediate surroundings of a randomly located point met plot location criteria, the point was marked with flagging tape to become the up-river / true right of valley corner of the sample. Plot boundaries were designated by measuring out two 10 m

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[5] This substrate feature represents a major difference in initial colonisation differences that could deflect the long term development trajectory.

lines at 90° to one another; the first always being perpendicular to the axis of the valley to avoid subjectivity of placement.

All fieldwork was undertaken during the period of January to March 2004 when plant species could be more easily identified owing to the presence of their reproductive parts.

5.3.2.4 Development stage ageing

Development stage ageing was conducted by a combination of reviewing historical data for the Fox Valley (Wardle 1973), extrapolation from information of ages in the Franz Josef valley (Stevens 1968) and sampling tree increment cores. The following three sections detail how these three means of deriving ages were applied to the sampled development stages.

5.3.2.4.1 Historical information

Wardle (1973) summarises all the recorded information known about the dates of historical positions of the Fox Glacier. It is possible to estimate ages for stages three and four from information provided by Wardle (1973). These estimates are based on historical accounts of glacial positions and vegetation assemblages at various points in the valley, combined with interpolation of historical glacial positions from maps of moraine remnants. However, the age for stage four so derived can not be very accurate because it relies on insufficiently detailed historical vegetation descriptions. Furthermore, the precise locations to which Wardle's information refers for both these stages is indeterminate. Therefore, in order to obtain more precise age estimates for stages three and four, increment cores were taken from woody species present on their surfaces (see section 5.3.2.4.3 below for details).

Development stage one is aged at six years from photos (courtesy of Fox Alpine Guides ltd.) showing the position of terminal moraine that marks the latest advance in 1998. The two sampling areas of stage one span the current course of the main Fox River near its exit from beneath the glacier (that is in a different position than in 1998, M. Brown pers. comm. 2004). The sampled area on one side is directly in front of a remnant of the 1998 terminal moraine, and on the other it is positioned the same distance away from the glacier as the moraine opposite. At the time of 1998 glacial maxima, the whole proximal area in front of the medial portion of the glacier had its vegetation destroyed and substrate re-worked by the action of glacial meltwater (M. Brown pers. comm. 2004). Photographic

evidence proves the surfaces of the two zones of sampling to have been formed at the same time even though one has no existing moraine evidence. It is important to note that it is assumed that similar levels of disturbance as have been observed closely in the proximal glacier foreland over the last few decades also occurred at all other surfaces during their formation, and at a similar scale. This assumption forms the basis of the assertion that the zone within 50 m of surface boundary is of approximately even age. Furthermore, the detailed and accurate accounts available of the geomorphic processes that formed the stage one surface (Alpine Guides Fox Glacier staff pers. comms. 2004) shed light on the processes which may have also formed surfaces of stages three and four. This is because those sites positions in the valley floor would also have been directly in front of the glacial terminus at the time of the last retreat (Wardle 1973; Coates & Chinn 1992).

5.3.2.4.2 Extrapolation from Franz-Josef chronosequence

The oldest development stage studied within the Fox Valley (DS 6) has no historical records. Neither is it possible to derive an age from tree cores owing to the approximate age, as estimated from local rates of glacial movement (Stevens 1968; Burrows 1990; Coates & Chinn 1992; Almond et al. 2001), being far older than the sum of the colonising time and individual life-span of the longest living species present (*Dacrydium cupressinum*).

Therefore, Stevens (1968) work in the Franz-Josef glacial valley provides the best information for placing an age estimate on stage six. Stevens used the change in chemical and physical characteristics during soil development to estimate the age of his chronosequence study surfaces. By using soil development characters Stevens was able to estimate age for sites up to c. 120,000 years old, a much longer time scale than is possible by using tree increment cores alone.

Since the Franz-Josef & Fox Glaciers share a very similar climate and gross morphology (distributions of accumulation versus ablation zones as well as sub-glacial valley topography), it is reasonable to assume that the rates of flow and timings of historical advance and recession were similar. Thus, I have assigned an approximate minimum age of DS 6 to be equal to the most similar of Stevens' sites in relation to altitude and distance away from the glacier terminal face. The resultant age estimate is c. 5,000 years.

Confirmation of this age being a reasonable estimate comes from observations of soil cores taken that indicated the soil at DS 6 is of a yellow-brown gley podsolic type

because the formation of a gleyed layer is estimated to take place after 2,000 years in this environment (Burrows 1990).

5.3.2.4.3 Tree increment core analysis

Increment cores taken by Dr. P. Wardle from development stage five (Wardle 1973) give an accurate age estimate for this stage. In order to improve upon the accuracy of ages derived from historical information (Wardle 1973) only (stages three and four), and to get an estimate for stage two, I took tree increment cores from development stages two, three and four. In addition, sampling increment cores enabled the testing, to some extent, of my field sampling assumption that all samples within 50 m of the surface boundary are of equal age. All three stages sampled are young enough to have extant first generation individuals of species characteristic of early development stages whose colonisation times could be reasonably accurately estimated.

A total of 60 cores were taken from the largest individuals with non-eccentric trunk cross sections of various species (*Pittosporum colensoi, Melicytus ramiflorus Weinmannia racemosa, Coriaria arborea, Olearia avicenniifolia, Carpodetus serratus, Carmichaelia arborea*) in the immediate vicinity of samples within each surface. Cores were taken at breast height, except for those from development stage two that were taken just above ground height as only young individuals of tree tutu (*Coriaria arborea*) were available. Where possible, cores were placed so as to intercept the geometric centre and angled upwards towards the inside to minimise detrimental effects on the tree.

Once taken, cores were stored in straws in a refrigerator until they could be air dried at 40°C. Dried cores were mounted and prepared using progressively finer grades of sandpaper until a smooth polish was obtained. Rings were counted using a stereo microscope.

Norton et al. (1987) suggest a method for estimating the missing radius where the chronological centre of the tree was not intercepted by the core. This relies on the presence of a clear arc formed by tree rings. The arcs are extrapolated to a circle using a compass, the radius of which is equal to the distance 'r' to the actual chronological centre. Each r distance was then transformed into an approximate number of rings using the average value for distance between rings in its core sample, following the method of Duncan (1989).

Where neither the chronological centre nor any arcing tree rings were found, it was only possible to estimate the distance to the geometric centre of the tree. This was done by

converting the difference between the tree radius and the length of the core (calculated from the DBH field measurement) into years through dividing it by the average inter-ring spacing throughout the core (e.g.Norton et al. 1987).

Out of the 60 cores taken in the field from woody species, 43 had distinct enough rings after preparation to be countable with confidence that negligible numbers of rings present were being missed or double counted. Each surface young enough to still have extant colonising species' individuals present was sampled. Cores of the fastest colonising species were found to consistently yield the greatest increment count of the various species sampled. Because conditions only persist for such species for a short window of time after the primary disturbance (Wardle 1980b), there is little doubt that the individuals cored were establishing themselves at a reasonably predictable time since disturbance. Furthermore, the previous observation combined with their relatively short life span (Wardle 1980b) means they must be first generation individuals.

To obtain the final figure for the estimates of tree age, a species specific number was added. This number corresponds to the sum of approximate times for growth to height of coring and time to first colonisation after the disturbance event that are shown in Table 5.3. These times were estimated from many of my field observations throughout the Fox Valley of species growth rates and colonisation times from younger surfaces where the age was known, including surfaces identified by Wardle in his 1973 paper, but whose extent was too limited to be sampled using the experimental design of this study.

Species	Time to colonisation	Growth time to coring height (yrs)
Carpodetus serratus	9	25
Carmichaelia arborea	4	2
Coriaria arborea	2	5
Melicytus ramiflorus	7	25
Olearia avicenniifolia	8	4
Pittosporum colensoi	9	15
Weinmannia recemosa	12	30

Table 5-3 Estimates used for time not accounted for by counting growth rings for each species sampled in order to estimate total age of surfaces.

It is recognised that incremental growth rings are not necessarily produced annually in the environment prevailing at the study site. This results in either missing rings, or,

double rings, neither of which can be quantified with the ring counting methods used here. Also, it is not possible to estimate the proportion of incomplete growth rings that may not be present in any particular core without taking whole tree cross sections[6], a practice not permitted within Fox Valley as it is located within a National Park. Therefore, all age estimates based on increment cores are considered to be minimum age estimates.

5.3.2.5 Measurement of environmental variables

Environmental data were recorded, with the aim of characterising as many as practical of the key features of the physical environment considered to possibly affect vegetation development. Physical descriptors recorded include; altitude, slope, soft sediment depth (SSD) and physiography. Altitude, slope and SSD were recorded using standard thesis methods. Physiography was visually estimated and recorded as a nominal variable with a value of one to four respectively for the categories: convex, concave, linear and undulating. The substrate variables median size and percentage cover of rocks[7] were measured by observing exposed rocks that protruded above the surface of the main substrate matrix of either soil or soft sediment.

Grazing effect of introduced animals was at low levels, was assumed to be even among development stages, and, is difficult to quantify, therefore it was decided to be not worth measuring.

5.3.2.5.1 Analysis usage limitations of environmental variables

Ideally, all environmental variables would be robust for inclusion in multivariate analyses to check correlations with the main floristic gradients among development stages. Unfortunately, SSD, median size and percentage cover of rocks are applicable only to investigate the effect of substrate differences on floristic variance among replicate samples within each stage. For median size and percentage cover of rocks this is so because

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[6] There are no published data on missing ring proportions for the species cored in this study from a similar climatic regime.

[7] A rock is defined as a substrate particle larger than 5 cm diameter.

measurement of among stage differences was confounded by progressive soil development. For SSD, it is because there is no way of differentiating between the proportion of SSD that is soil or inorganic fines. Therefore, whilst the pattern of variation of SSD among stages approximates the pattern of soil accumulation, it does not measure soil depth. However, it can be used to estimate the effect on floristic variance of variation in fine sediment deposition among replicate samples per stage. This is based on the assumption that soil development would have occurred at the same rate among samples of the same age.

5.3.2.6 Soil sampling for pH & organic carbon

Soil sampling followed standard thesis methods. Development stages one and two were not sampled owing to their lack of a developed soil profile.

5.3.2.7 Cover abundance estimation

Cover abundance of all vascular plant species was estimated using standard thesis methods. With the range of vegetation types present in the chronosequence at Fox, up to seven tiers per sample were identified by the following strata descriptors; ground, shrub, small tree, sub-canopy, canopy, emergent and epiphyte.

5.3.2.8 Plant species identification

Plant identification followed standard thesis methods.

5.3.3 ANALYSIS TOOLS

The analysis tools employed for the Fox data set are the same as those used for the other two study sites.

5.3.3.1 Exploratory data analysis (EDA)

EDA followed the standard thesis methods. Prior to all multivariate analyses, all variables were transformed which displayed a functional relationship between value and variance. Transformations adopted were; the natural log function for organic carbon and rock cover (suitable because they are measured in percentages) and cube root for importance score (because it is a measurement in units of volume). In addition, DCA axis one values were transformed by the natural log.

5.3.3.2 Vegetation description

Following standard thesis methods, the average plant assemblage present in each development stage is characterised by three means: a compositional summary table is calculated, a specific name is derived and the key structural features are described.

5.3.3.3 Ordination – DCA & DCCA

The methods of Detrended Correspondence Analysis (DCA) and Detrended Canonical Correspondence Analysis (DCCA) were used to describe the pattern of floristic variation among all the samples and to assess relationships between sample floristics and measured environmental variables following standard thesis methods.

Not all environmental variables measured were suitable for inclusion in the DCA analysis. Soil chemical variables were not included because of the missing values for the two younger surfaces with no soil profile. The substrate variables SSD, rock median size and percentage cover of rocks were not included because their values only truly represent variation within, rather than among, stages. This renders the ordination package used unable to test the relationship between floristics and these variables because it cannot provide individual correlations of environmental variables with sub-sets of samples. The remaining environmental variables (age, slope angle, physiography and altitude) were subjected to a preliminary DCA run and output accuracy warnings checked. There were no warnings. Of the environmental variables included within the DCA analysis, only physiography was excluded from the DCCA analysis because it is measured on a nominal scale and is therefore unsuitable for such direct ordination methods (ter Braak & Smilauer 1998).

5.3.3.4 ANOSIM (ANALYSIS OF SIMILARITIES)

A pair-wise ANOSIM was performed on the floristics of each development stage pair, following standard thesis methods.

5.3.3.5 Regression part one

Regression analysis is used to investigate two questions pertaining to the Fox data set. These are covered in two separate methods and results sections:

- Part one covers:
    - Do any of the selected environmental variables (substrate and soil variables) explain a significant amount of either of the main floristic gradients?

- Part two covers:
    - Are univariate indices dependent on age, how strong is their response and do linear or second order polynomial regression models fit the response trajectory best?

A full explanation of regression methods can be found in Chapter two.

5.3.3.5.1 General methods for part one and part two regression analyses

Prior to all regression analyses (except those involving single stage data sets) steps were taken to ensure each variable was sufficiently homoscedastic among stages. Firstly, any variables with a functional relationship between value and variance were transformed; these were organic carbon and DCA axis one (by natural log) as well as importance score (cube root). Secondly, the homogeneity of variances among the sample groups for each stage was quantifiably assessed for each variable (including those transformed) by computing Bartlett's test (Bartlett 1938) using GenStat. A 'pass' result for Bartlett's test, meaning homogenous variance, was set at the critical value of ≥ 0.001. All variables that failed (Table 5.4) were automatically assigned weightings to each stage prior to regression analysis.

	Bartlett's test results		
Univariate index	χ^2	**'p' value** (df =5)	**Requires weighting?**
pH	4.26	0.235**	N
Organic carbon % *	6.27	0.104**	N
Importance score (m^3 cover)*	22.95	<0.001	Y
Species density (n per 100m^2)	12.53	0.028	N
Simpson's diversity (-lnD)	17.29	0.004	Y
Simpson's evenness ($E_{1/D}$)	23.52	<0.001	Y
Distance from lognormal (ΔL)	8.85	0.115	N
Shannon's growth form diversity (H')	34.36	<0.001	Y
Functional richness (Fcr)	108.32	<0.001	Y
Functional evenness (FRO)	1.32	0.933	N
Functional difference (V)	28.32	<0.001	Y
Taxonomic distinctness (Δ*)	32.64	<0.001	Y
DCA axis one (S.D.)*	76.73	<0.001	Y

Table 5-4 Results of Bartlett's test for homogeneity of variance for all variables subjected to regressions not restricted to individual development stage sample sets. '*' denotes that a transformed version of the variable was used in the test. The critical value for rejection of homogeneity of variance was $p \leq 0.001$. '**' denotes three degrees of freedom, rather than the normal five.

Outputs from all regressions (part one and part two analyses) were screened for error messages regarding data points with high leverage; none were notified. Some outlying data points with large residuals were identified but these were considered to be acceptable owing to their lack of leverage effect.

5.3.3.5.2 Testing the influence on floristics of environmental variables not included in correspondence analysis.

The testing of environmental variables not included in correspondence analysis (pH, organic carbon, soft sediment depth, surface rock size and surface rock cover) concludes the investigation of the relationship between environmental variables and floristics because no variables apart from age were significantly correlated with either DCA axis one or two. Slightly different methods were used for the two soil chemical variables than for the three substrate variables. This is because the chemical variables were tested against the entire floristic gradient whereas the substrate variables were tested against floristic variation within each stage individually.

For the regressions involving the two soil chemical property variables, the standard stepwise methods as described in Chapter two were used. This involved the two variables being added sequentially to models of DCA axis one and two to test the strength of their relationship with floristic variation with that explained by age already taken into account (by manually adding age to the models as a fixed variable).

For the regressions involving the three substrate variables, standard thesis methods for stepwise regression were used, except that age was not included in the models of DCA axes one because a separate run was made for each development stage (by restricting the data set to only samples from within each stage). Also, because a separate model was applied to data from each development stage, no testing for homogeneity of variance among stages was required for the environmental variables in these analyses. Section 5.3.2.5.1 explains why these variables were only suitable for testing their effect on floristic variation within (rather than among) development stages.

5.3.3.6 Univariate indices of vegetation development

A range of univariate indices were calculated using standard thesis methods. All indices applied to the Fox data set are common to all study sites except the two soil properties (organic carbon and pH) which are relevant to the two forest study sites only.

5.3.3.6.1 Regression part two analysis

Testing dependence of univariate indices upon age.

Regressions were applied using standard thesis methods to assess the relationships between each individual univariate index of vegetation development and age. Each index was sequentially fitted to first linear and then quadratic models. Finally, a test was performed to calculate which model had the significantly better fit.

5.3.3.7 Ordination- Principal Components Analysis (PCA)

The two PCA analyses follow the standard thesis methods. Firstly, a PCA analysis was performed on the data for all univariate indices using the same transformations of the indices values as were used for the regressions. Secondly, a PCA analysis was performed on species abundance data using default options.

5.4 RESULTS

The format of results follows the same order as has been used both in the general methods, Chapter two, and, in the methods section of this chapter.

5.4.1 FIELD DATA

Results from field data include ages for each development stage and a summary of the environmental variable data.

5.4.1.1 Development stage ages

Tree increment core analysis results yielded age estimates for development stages two, three and four. Historical information gives an accurate age for stage one, and, extrapolation from ages of the Franz Josef sequence give an estimate for the age of stage six. Therefore, with the exception of stage five, surface ages estimates adopted for use in this study are based on research undertaken in this study. Stage five is deemed to be the most reliable of the age estimates made by Wardle (1973) for surfaces sampled in this study (see sections 5.3.2.4.1/3). This is because it is the only one based on tree increment core samples. Wardle's age estimates for other stages are included for reference and comparison only. Development stage age estimates from all sources are given in Table 5.5; of those adopted all which are not derived from direct observation (DSs 2-6) are regarded as minimum estimates (see sections 5.3.2.4.2/3 for an explanation).

Development stage in chronosequence	Surface ID code	age estimate after Wardle (1973)	age estimate from work of this study	age estimate (=minimum age) used for analysis
1	J	-	6	6
2	I	-	30	30
3	G	70	73	73
4	E	165*	159	159
5	B	400	-	400
6	A	-	5000	5000

Table 5-5 Table of development stage age (minimum time since colonisation) estimates from different sources of each positively identified surface in the Fox Valley. '*' denotes my interpolation from P. Wardle (1973) where sufficient evidence for an age estimate was given yet none was made by P. Wardle himself.

The figures derived in this study broadly agree with the estimates derived form Wardle's work (Table 5.5). The estimates from increment cores for the younger stages (two, three and four) are expected to be more accurate than those for the older stages (five and six). This is because there is less uncertainty of the time to colonisation for these early colonising species owing to there being a low spatial variation in conditions for colonisation before any significant vegetation cover has formed.

5.4.1.2 Environmental variable variation among development stages

Results in Table 5.6 and Figure 5.7 show that none of the environmental variables measured, except soft sediment depth[8], have a pattern clearly dependent on age. There is an unknown proportion of the variation in soft sediment depth, both within and among development stages, that is due to deposited amounts of inorganic fines, either during initial surface formation or during subsequent floods. Yet the pattern is assumed to be primarily reflecting progressive soil development.

Altitude has little variation within development stages because sampled surfaces were by design virtually flat features. Altitude has a small variation among development stages because although distance down valley increases with age, the surfaces are not necessarily located on the valley floor. Slope variation within and among development stages is minimal. Rock cover and rock size are highly variable within development stages and the variation among development stages suggests some differences in initial substrate, however, the general trends for rock cover to decrease and rock size to increase (until DS 4) with age of surface are both associated with obscuring effect of increasing soil depth.

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[8] Soil chemical properties are dependent on age but they are treated as univariate indicators of vegetation development rather than environmental variables.

Physiography class	Development stage					
	1	2	3	4	5	6
Undulating	3	0	1	0	4	0
Convex	0	1	0	0	0	0
Concave	0	0	0	0	0	0
Linear	3	8	8	9	5	9

Table 5-6 Counts per development stage for the number of samples designated within each of the physiography classes.

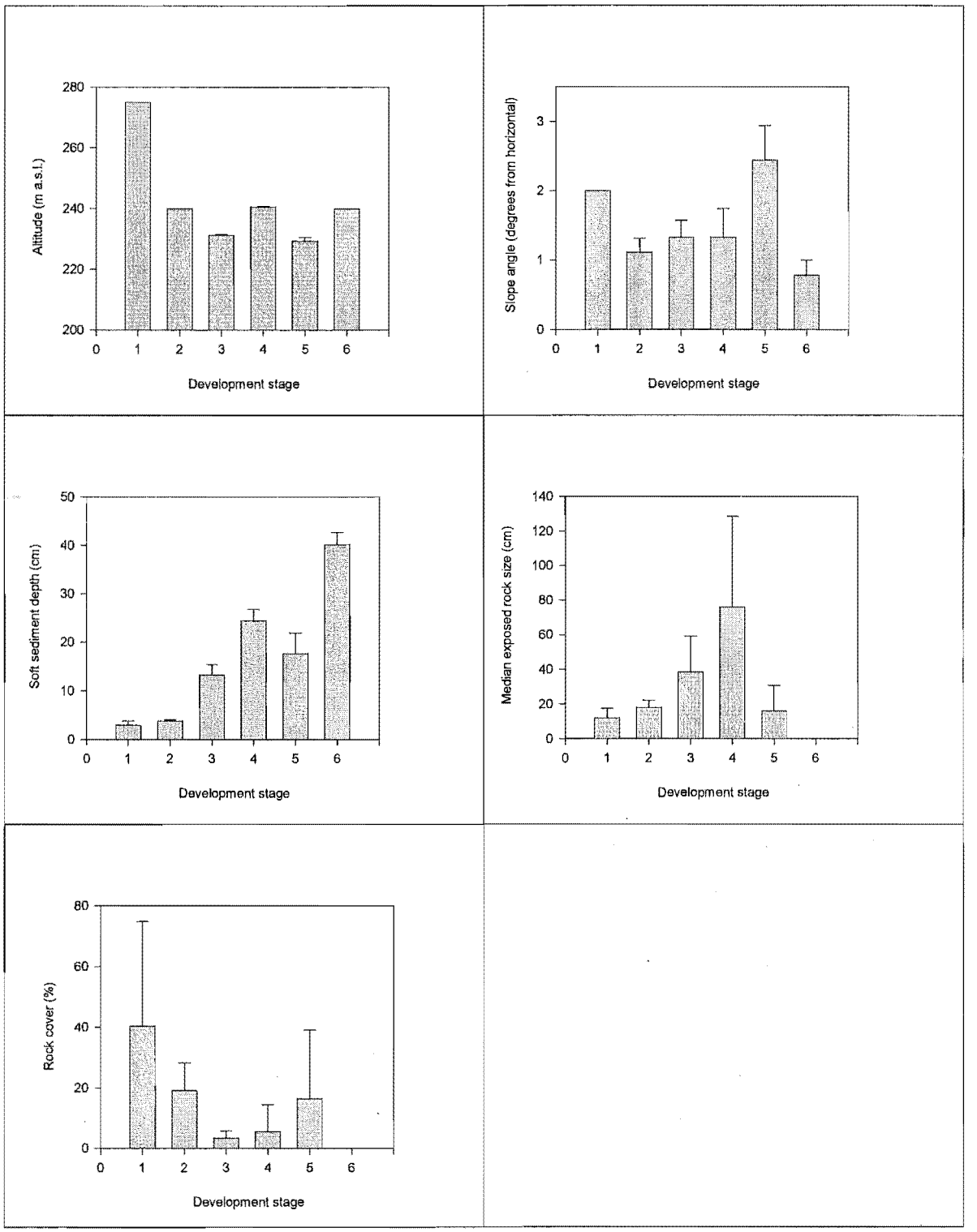

Figure 5-7 Bar graphs of all environmental variables (except physiography due to it being measured on a nominal scale) values per development stage. Means per development stage and standard error about the means are presented.

5.4.2 RESULTS OF ANALYSES

All results are based on the analysis of vascular plant species data obtained for each sample, some analyses also combine measurements of environmental characteristics (see Table 2.1, Chapter two for a summary analysis data inputs).

5.4.2.1 Vegetation description

In this section, the plant assemblages of each development stage are named and described. Table 5.7 overleaf summarises the species composition of each stage and broadly illustrates vegetation development in terms of changes in species abundances and species turnover among stages.

Species	Development stage 1	2	3	4	5	6
Carmichaelia arborea	**5.6**	8.6	2.9			
Raoulia tenuicaulis	**2.0**	2.6				
Coriaria arborea		**61.7**		4.9		
Hebe salicifolia		2.9	2.4			
Olearia avicenniifolia		3.2	**37.1**			
Rytidosperma gracile		2.4				
Lachnagrostis lyallii		2.3				
Epilobium brunnescens		2.1				
Schefflera digitata			9.9	**34.0**	**25.9**	
Pittosporum colensoi			6.5			
Coprosma lucida			4.2			
Aristotelia serrata			4.8	4.8		
Polystichum vestitum			2.4			
Cyathea smithii			3.2	**31.0**	17.0	
Melicytus ramiflorus				17.1	8.9	
Carpodetus serratus				**25.8**	4.0	
Asplenium bulbiferum				**28.6**	**22.6**	
Blechnum chambersii				2.5		
Weinmannia racemosa					**23.2**	**37.4**
Metrosideros umbellata					**21.0**	6.1
Griselinia littoralis			**16.6**	5.1	18.0	
Nertera villosa				2.6	5.4	
Myrsine australis					4.5	
Cardiomanes reniforme					2.4	
Prumnopitys ferruginea						**30.3**
Blechnum discolor						**24.5**
Dacrydium cupressinum						14.5
Hedycarya arborea					3.6	13.5
Metrosideros diffusa						8.4
Metrosideros fulgens						7.3
Ripogonum scandens						7.0
Dicksonia squarrosa			3.8		5.8	7.0
Raukaua simplex						6.5
Metrosideros perforata						6.0
Coprosma foetidissima						3.1
Microsorum pustulatum						2.8

Table 5-7 The mean total (summed values for all tiers) percentage cover per development stage of species with a total mean cover of ≥2 % in at least one development stage. Values indicated by bold type highlight dominant species (in any tier) which appear in the compositional part of the name of the development stage they are present in. The order of species in the table corresponds to a rough representation of species turnover through the chronosequence.

5.4.2.1.1 Development stage plant assemblage descriptions

Each development stage name is comprised of two parts; the first referring to the dominant species, and the second to the structural appearance. Table 5.7 summarises the species composition of each assemblage. Dominant species that appear in the stage name are in bold type, the remainder give an impression of the assemblage structure to compliment the descriptions that follow.

Development stage one: [*Carmichaelia arborea / Poa novae-zelandiae*] Gravel field

This stage was characterised by the sparsely scattered *Carmichaelia arborea* shrubs which grew to c. 1.5 m on average. They form a stark physiognomic contrast to the reasonably floristically diverse herb layer dominated by native grasses and cushion plants (*Raoulia* spp.). The ground layer was mainly composed of gravels with varying quantities of rocks and occasional boulders.

Development stage two: *Coriaria arborea* – [*Carmichaelia arborea*] Shrubland

Stage two was characterised by the cover dominance of tree tutu (*Coriaria arborea)*, a shrub species present in the previous stage as seedlings only. The shrub canopy reached an average height of c. 2.5 m and had significant amounts of other shrub species such as *Carmichaelia arborea* and *Hebe salicifolia.* There was a developing sub canopy including *Olearia avicenniifolia, Griselinia littoralis* and *Schefflera digitata.*

More open areas were characterised by a floristically diverse array of native tall tussock grasses, shrubs and herbs, including *Chionochloa flavescens / Cortaderia richardii*, *Coprosma* spp. and *Gnaphalium* spp. respectively. *Raoulia* spp. mats were persistent in open areas but had become almost shaded out. The ground layer beneath the tree tutu cover had many seedlings of low forest species such as *Schefflera digitata*, *Pittosporum colensoi* and *Weinmannia racemosa*, as well as a few small specimens of fern species characteristic of a successional forest ground layer e.g. *Polystichum vestitum* and *Blechnum novae-zelandiae.*

Development stage three: *Olearia aviceniifolia / Griselinia littoralis* Scrub

Stage three was characterised by a dense canopy of tall shrub species of remarkably even height reaching five to six metres high. Canopy cover was dominated by *Olearia aviceniifolia*, with *Pittosporum colensoi, Aristotelia serrata, Carmichaelia arborea* and

Hebe salicifolia also common. *Coriaria arborea* was present in the canopy but most individuals were dying out. Epiphyte species such as *Hymenophyllum* spp. and *Microsorum pustulatum* were common but had a very low abundance.

The abundant sub-canopy reached up to c. three metres and was dominated by *Griselinia littoralis* and *Schefflera digitata* with a significant component of tree ferns and *Coprosma* spp. Conspicuous species in the shrub layer were the forest lily (*Astelia fragrans*) and the tall tussock *Cortaderia richardi*. The ground layer had a variable but usually sparse cover of herbs dominated by *Nertera* spp.

Development stage four: *Carpodetus serratus / Schefflera digitata- Cyathea smithii / Asplenium bulbiferum* Low forest

Development stage four was characterised by a closed canopy of low successional forest of variable height but averaging c. eight metres. *Carpodetus serratus* was co-dominant with *Melicytus ramiflorus* in the canopy, with the former often emergent. The remainder of the canopy was lower and mostly continuous with the sub-canopy; the most abundant species being *Schefflera digitata* and the tree fern *Cyathea smithii*, with *Griselinia littoralis and Aristotelia serrata* commonly occurring. A few highly leaning individuals of *Coriaria arborea* still persisted. Epiphytes had increased in diversity from the previous stage but still did not have a high abundance.

The shrub layer had a dense cover of *Asplenium bulbiferum* with other fern species and tree saplings making up most of the remainder. The ground layer had a sparse cover of *Nertera* spp. and moss in occasional patches.

Development stage five: *Weinmannia racemosa – Metrosideros umbellata / Schefflera digitata / Asplenium bulbiferum* Forest

Development stage five was a tall successional forest characterised by a canopy of even height (~ 20 m) co-dominant *Metrosideros umbellata* and *Weinmannia racemosa*. The canopy was punctuated by tree fall gaps created by individuals of either of the co-dominants that had reached the end of their lifespan.

The sub canopy and small tree layers were intergrading and had a high diversity of woody species with *Weinmannia racemosa* being most abundant. *Griselinia littoralis*, *Schefflera digitata*, *Cyathea smithii* were very common whereas *Melicytus ramiflorus*, *Pseudopanax* spp. and *Coprosma* spp. were common. Saplings of the podocarps *Prumnopitys ferruginea* and *Dacrydium cupressinum* were present but rare. Tree fall gaps

had roughly the same composition as the sub-canopy with the conspicuous addition of lianes and vines. Epiphytes had a high diversity and reasonable abundance.

The shrub layer was relatively open and dominated by *Asplenium bulbiferum* and the tree fern *Dicksonia squarrosa*. The ground layer had a sparse cover dominated by ground ferns, mainly *Blechnum* spp.

Development stage six: (*Dacrydium cupressinum*) / *Weinmannia racemosa* - *Prumnopitys ferruginea* / *Blechnum discolour* Tall forest

Development stage six was characterised by a very tall canopy of mature forest dominated by *Weinmannia racemosa*, with *Dacrydium cupressinum* being a conspicuous and common emergent reaching up to 35 metres in height. The most striking features were perhaps the physiognomic complexity of the habitat, the luxuriant and diverse epiphyte layer that covered almost all available trunk space and the often impenetrable tangle of lianas and vines that commonly descended from the canopy to the ground in tree fall gaps. *Weinmannia racemosa* and *Prumnopitys ferruginea* were co-dominant in the distinct sub canopy. The small tree layer was variable in height, extending up to 12 m, and included a high diversity of species; *Hedycarya arborea*, *Raukaua simplex* and tree ferns dominated, whereas *Pseudopanax* spp., several *Coprosma* spp. and *Schefflera digitata* were common.

The shrub layer was dominated by the distinctive crown fern (*Blechnum discolor*), and *Asplenium bulbiferum* was common. The ground layer was dominated by extensive mats of climbing *Metrosideros* spp. that were interspersed mainly with moss as well as the occasional tree seedling or herb species.

5.4.2.2 Ordination – DCA & DCCA

Ordination was used to graphically represent the pattern of floristic variation among and between development stages, as well as to establish if age is correlated most strongly with the main floristic gradient.

The proportion of the total variation in the species data that was explained by the first four axes of the DCA unconstrained ordination is 35.0 %. This figure is within the expected range for species abundance data and an ordination of this power can be very informative (Gauch 1982).

The eigenvalues are a measure of the importance of each ordination axis. Values of over 0.5 denote a good separation of the samples along the axis (Jongman et al. 1995). Eigenvalues also indicate the relative proportion of total species variation accounted for by each axis gradient (ter Braak & Smilauer 1998). The eigenvalues for each of the four DCA axes were 0.860, 0.239, 0.136 and 0.085 respectively. As axes three and four were small compared with the first two they can be ignored; the biologically relevant information being expected to be displayed by the first two (Jongman et al. 1995). Therefore, Figure 5.8 that displays DCA sample scores incorporates axis one and two scores only. Furthermore, the main conclusions drawn from the ordination results can be taken from axis one information because it comprised a large proportion (65 %) of the variance of species data explained by the first four axes of the ordination (as compared to 18 % for axis two).

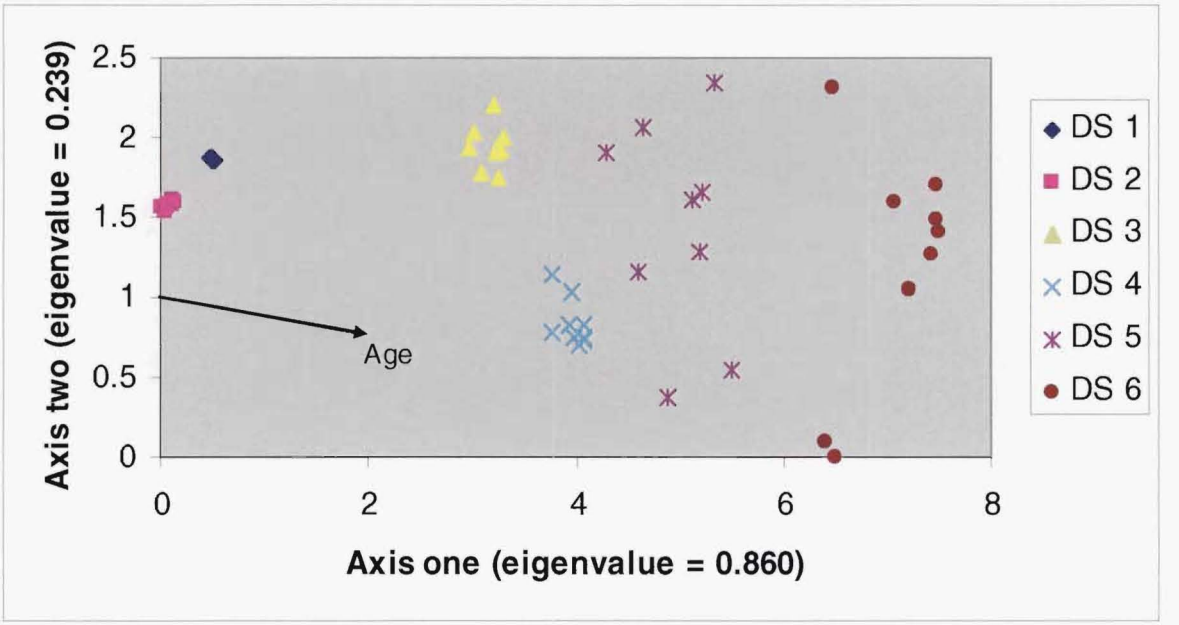

Figure 5.8 Axes one and two of the DCA ordination including the six chronosequence development stages. The biplot vector for the only environmental variable a with highly significant ($p \leq 0.001$) correlation coefficient (r) is shown. The length of the vector is proportional to the 'r' value and it's direction indicates the direction of maximum change of the continuous variable (ter Braak & Smilauer 1998).

The gradient length of DCA axis one given in Table 5.8 indicates that an almost two-fold turnover of species occurred along the main vegetation development gradient. The first and second DCA axes eigenvalues and gradient lengths were similar to those for DCCA (Table 5.8), showing that constraining the ordination to be a linear combination of the measured environmental variables did not grossly affect it. This indicates that all environmental variables that have an important influence on floristics were included in the analysis. The correlation coefficient between axis one DCA and DCCA ordination sample scores (Table 5.8) was very high. This is interpreted as the floristic variation explained by DCA axis one being mostly accounted for by the environmental variables included in the DCCA analysis. The correlation between axis two DCA and DCCA scores, although significant, was considerably lower than that for axis one. In ecological studies this is common and probably reflects that DCA axis two represents floristic variation owing to unknown or unmeasured environmental variables that have not been included in the analysis (Jongman et al. 1995). However, because DCA axis two did not account for a high proportion of floristic variation, these variables are not considered important.

Axis	Eigenvalues		Gradient lengths		Correlation coefficient (r_p)
	DCA	DCCA	DCA	DCCA	
1	0.86	0.77	7.51	3.92	0.97***
2	0.24	0.17	2.35	0.91	-0.58***

Table 5-8 Eigenvalues and gradient lengths (SD) for the first two axes of the DCA & DCCA ordinations. Pearson product moment correlations (r_p) are given of the first and second DCA axes sample scores with the first and second DCCA axes sample scores: '***' denotes significance at the critical value $p \leq 0.001$; d.f. 49.

The graph in Figure 5.8 clearly shows that the ordination of species abundance data separated the samples into floristically distinct groups corresponding to the development stages. The order of the groups from left to right corresponds with increasing age except for development stage one. Dispersion within the groups along both axis one and two increases from the youngest to the oldest.

Table 5.9 details the correlations between environmental variables included in the DCA analysis and the floristic gradients represented by axis one and two. The only environmental variable among this group that was significantly correlated with a floristic

gradient was age, with axis one. This result indicates that axis one of the ordination represents mainly an age gradient. This conclusion is strengthened by the very strong correlation between the first axes of DCA & DCCA that suggests there were no environmental variables of importance to floristics other than those included in the analysis. Therefore, since most floristic variation was accounted for by axis one, it is

Environmental variable	Correlation coefficients	
	Axis 1	Axis 2
Age	0.794***	-0.155
Slope angle	-0.093	0.160
Physiography (r_s)	0.118	0.106
Altitude	0.078	-0.263

Table 5-9 Correlation coefficients calculated between environmental variables and the first two DCA ordination axes sample scores. Pearson product moment correlations, copied from 'inter-set' correlations in the ordination output information, are given where data is of interval scale: '***' signifies significance at the critical value of 0.423 ($p \leq 0.001$[1]; df=49). A non-parametric Spearman's rank correlation (r_s) is given for 'physiography' only[2]: critical value of 0.434 ($p \leq 0.001$ df=49).

reasonable to conclude that age is the main driver of floristic change. This conclusion, supports DCA axis one being used as a univariate index to represent the vegetation development gradient against time.

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[1] In discussing the correlations of environmental variables against the species data, only highly significant relationships ($P \leq 0.001$) are considered important. Although this may appear a relatively stringent requirement, with the sample size of 51 a just significant relationship ($p \leq 0.05$ yet ≥ 0.01) would be very weak (the minimum coefficient of determination (r^2) for a significant relationship in this case would be only 0.17).

[2] A Spearman's rank correlation is calculated for the nominal scale variable 'physiography', because the default parametric correlation used in the CANOCO programme conveys little information for such variable types (ter Braak & Smilauer 1998).

5.4.2.3 Pair-wise ANOSIM of development stage floristics

Table 5.10 displays the ANOSIM results for all pair-wise development stage comparisons. The p values for all comparisons are highly significant, as would be expected from how separated the development stage sample groups are in the DCA ordination graph (Figure 5.8). However, the important message is in the R values, which, unlike p values, are "not unduly affected" by the number of replicates in the groups being compared (Clarke & Gorley 2001a), and give an absolute measure of how separated the floristics of the development stages are. R values are high for all comparison groups showing that the development stages of the chronosequence that are sampled have sufficient separation along the successional gradient to be used to describe the pattern of change in the univariate indices with time since disturbance. In the case of DS1/2 and DS 2/3 comparisons (R=1), the interpretation is that all the replicates within each stage are more similar to each other than they are to any replicates from the other stage within the comparison. With respect to DS 3/4 and DS 5/6 comparisons (R=>0.75) the stages are considered to be very well separated. Lastly, the value for the DS 4/5 comparison (R=<0.75) shows a slight overlap between stages but confirms they are still clearly different.

Pairwise comparison of development stages	'R' value	'p' value
1/2	1	0.001
2/3	1	0.002
3/4	0.999	0.001
4/5	0.715	0.001
5/6	0.842	0.001

Table 5-10 Table of ANOSIM p & r values per pair-wise development stage comparison where the null hypothesis is no differences between stages.

5.4.2.4 Regression part one: Testing the relationship between the environmental variables that were not included in correspondence analysis and floristics

5.4.2.4.1 Soil chemical properties

Both of the soil chemical properties were automatically rejected by GenStat when added to the stepwise regression model that tested for important explanatory variables of floristics (with the effect of age taken into account). Owing to the default options of the stepwise procedure, this means that their addition into the model would have caused a negligible change in the residual mean square values (far below significance level). Thus,

it is concluded that neither organic carbon nor pH are important explanatory variables of floristic variation within each stage.

5.4.2.4.2 Substrate variables

When added to the regression models individually, none of the three substrate variables were found to have a significant relationship with floristic variation within any development stage (i.e. none of them passed the threshold for remaining part of the model). The only significant result (Fpr = 0.034) was obtained with the combined effect of both soft sediment depth and surface rock size on development stage four floristics. However, this significance level represents a weak relationship.

5.4.2.5 Univariate indices of vegetation development

A total of 13 univariate indices of vegetation development have been derived. Each index has a value for each sample[3]. The observed results (means per development stage and standard error bars) for all indices are presented in the regression part two results section (5.4.2.6), together with overlaid regression curves modelling their response to age. In this section, Figure 5.9 presents results (in their untransformed state) for only the three indices whose values are on a transformed scale in the regression graphs.

Rank/abundance graphs per development stage are presented in this section also, because of the importance of the change in species RADs with respect to the response trajectories of the species diversity and distance from lognormal distribution indices.

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[3] Except for soil chemical properties for DS 1 & 2.

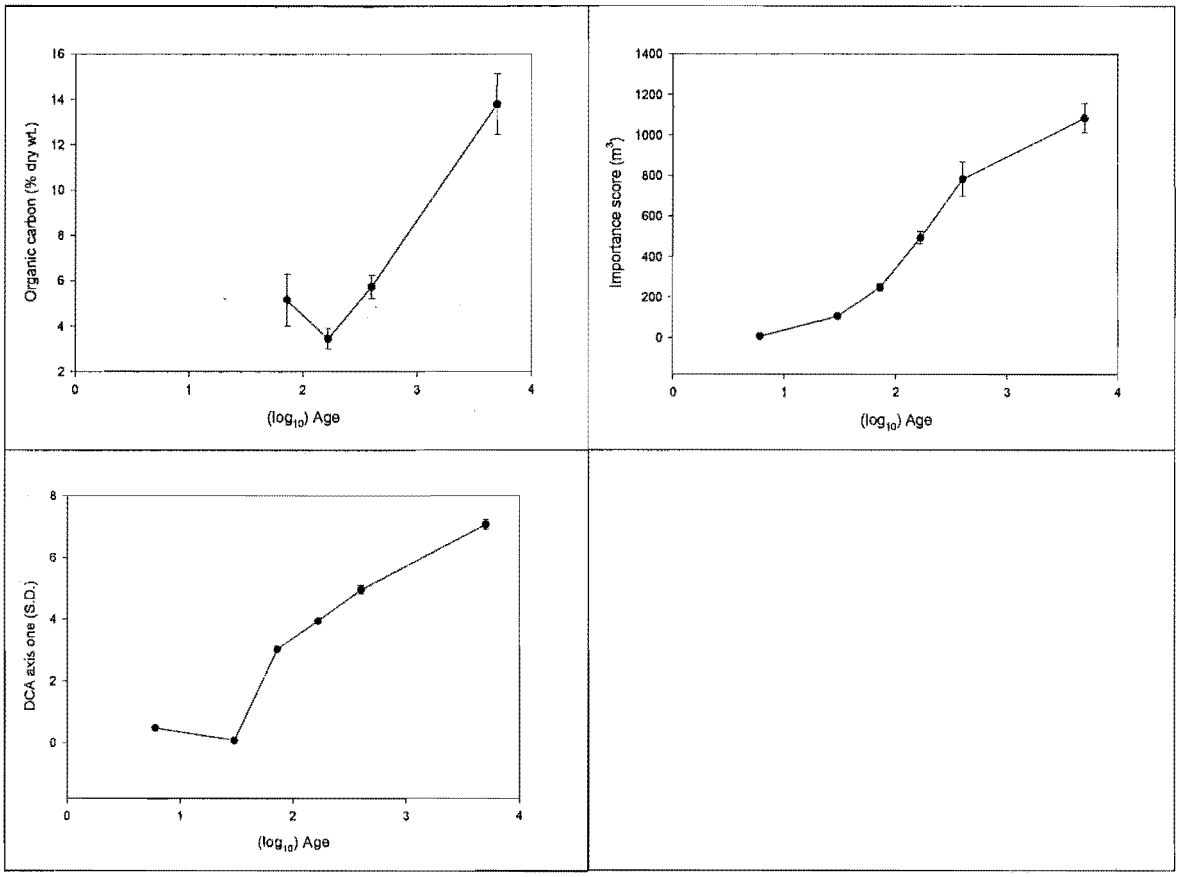

Figure 5-9 Untransformed mean and standard error of the mean per development stage for those univariate indices of vegetation development that were transformed for regression analysis (Organic carbon %, importance score, DCA axis one). Graphs for all indices not illustrated here are presented in the regression part two results (section 5.4.2.6).

5.4.2.5.1 Assemblage relative abundance distributions

Figure 5.10 below shows how the RAD changes along the vegetation development gradient. It can be seen that there is a progression over time from a curve that resembles the geometric series (DS 1) model through to something closer to the broken stick model (DS 2), and, by stage six, it has approached the lognormal model. This progression complements the results for the distance from the lognormal distribution (ΔL) index (Figure 5.11) which show a trend of decreasing distance with age.

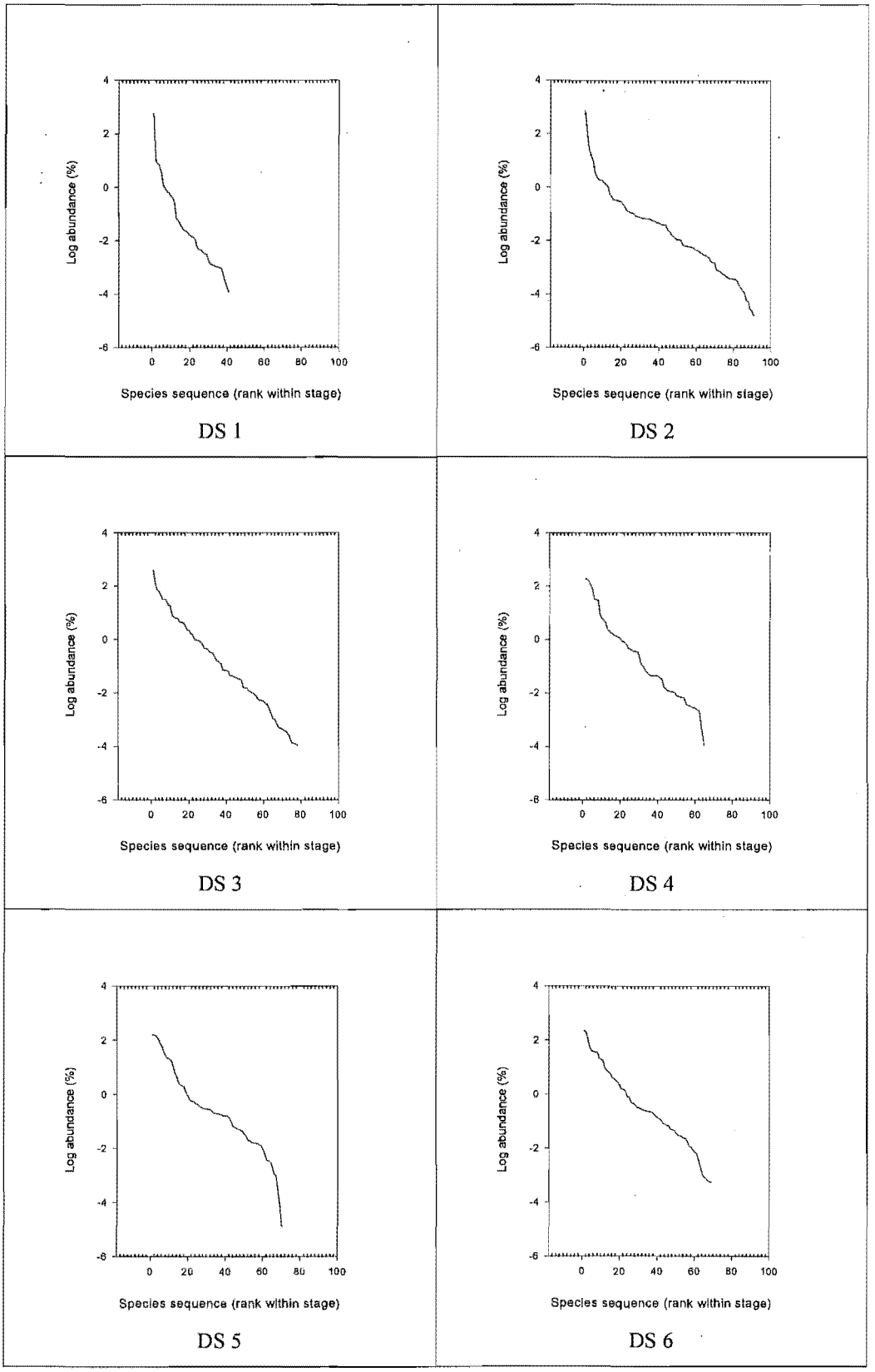

Figure 5-10 Rank/abundance plots (Log_{10} abundance versus species sequence by rank order) showing the average RAD pattern for each surface calculated by summing the abundances for each species for all the replicate samples within each surface.

5.4.2.6 Regression part two: Fitting regression models to index pattern of change

The results in Tables 5.11, 5.12 & 5.13 and in Figure 5.11 describe the relationship between each index and age in terms of the fit of observed data to either linear or polynomial regression models.

All linear regressions are highly significant (Fpr data) except for functional richness, species density and functional evenness. The relationships with age of these three exceptions are; highly insignificant, just non-significant and just significant respectively. This means that except for these three indices there is a significant directional trend in the data. In all cases of a significant linear regression, the standard error of the slope is low enough to give highly significant probability that the slope is valid (tpr data). The degree to which the linear regression model explains the observed pattern can be discerned by examining the coefficient of determination (r^2 data). Thus, indices with highly linear trajectories are: pH, importance score, Simpson's diversity and DCA axis one.

			Linear regression results					
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{49}**	**tpr**
pH	1.76	0.052	<0.001	84.5	-0.76	0.056	-13.6	<0.001
Organic Carbon (%) *	7.37	0.217	<0.001	52.3	0.71	0.105	6.8	<0.001
Sample import. score (m^3_{cover})*	46.25	0.944	<0.001	92.2	3.18	0.071	44.7	<0.001
Species density (n per $100m^2$)	3913	79.86	0.073	4.5	2.60	0.661	3.9	<0.001
Simpson's diversity (-lnD)	9.43	0.193	<0.001	79.7	0.67	0.022	30.2	<0.001
Simpson's evenness ($E_{1/d}$)	0.141	0.003	<0.001	40.8	0.05	0.003	14.5	<0.001
Distance from lognormal (ΔL)	4.32	0.088	<0.001	34.3	-0.25	0.035	-7.1	<0.001
Shannon's growth form div. (H')	10.58	0.216	<0.001	43.2	0.43	0.014	30.8	<0.001
Functional richness ($\%_{site\ trait\ range}$)	1711	34.92	0.432	**				
Functional evenness (FRO)	0.168	0.003	0.031	7.3	-0.02	0.009	-2.3	0.03
Functional difference (V)	240.4	4.906	<0.001	67.8	2.66	0.156	17.1	<0.001
Taxonomic distinctness (Δ*)	2679	54.67	<0.001	61.1	10.24	0.520	19.7	<0.001
DCA axis one (S.D.) *	96.47	1.969	<0.001	85.4	1.10	0.007	150.4	<0.001

Table 5-11 ANOVA results for testing the significance of regressions fitting a linear model to each univariate index separately with age. '*' denotes that the index values were transformed before applying regression analysis. '**' denotes that no variance was explained owing to the residual variance being greater than that of the dependent (response) variable; no further results are quoted in this case. Refer to Table 3.8 caption for an explanation of column headings.

The polynomial regression results in Table 5.12 help to quantify the extent and pattern of non-linear index trajectories. All indices, except functional evenness, have a significant polynomial regression, however this does not imply that the polynomial

regressions fit better than the linear ones. Polynomial slope significance (tpr) and a higher coefficient of determination than reported for linear regression implies that the pattern is better represented by the polynomial model. A big increase in the coefficient of determination between linear and polynomial indicates that the index trajectory has a high degree of curvature (e.g. species density and functional richness). Slope results do not relate directly to curvature because they are relative to the units of the x-axis. The F-test results in Table 5.13 below give a definitive answer as to which model fits best.

	Polynomial regression results							
Index	**SS**	**RMS**	**Fpr**	**r^2**	**Slope**	**Slope SE**	**t_{48}**	**tpr**
pH	1.69	0.05	<0.001	84.2	-0.127	0.11	-1.15	0.259
Organic Carbon (%) *	6.81	0.21	<0.001	54.6	0.366	0.222	1.65	0.109
Sample importance score (m^3_{cover})*	17.45	0.36	<0.001	97.0	-0.633	0.071	-8.9	<0.001
Species density (n per 100m^2)	3127	65.14	<0.001	22.1	-4.47	1.291	-3.48	0.001
Simpson's diversity (-lnD)	7.80	0.16	<0.001	82.9	-0.165	0.052	-3.17	0.003
Simpson's evenness ($E_{1/D}$)	0.140	0.003	<0.001	40.2	0.005	0.008	0.69	0.493
Distance from lognormal (ΔL)	3.23	0.067	<0.001	49.8	0.167	0.041	4.03	<0.001
Shannon's growth form div. (H')	9.69	0.202	<0.001	47.0	-0.147	0.069	-2.12	0.039
Functional richness ($\%_{site\ trait\ range}$)	1056	22.0	<0.001	36.5	-4.082	0.748	-5.46	<0.001
Functional evenness (FRO)	0.166	0.003	0.07	6.8	0.008	0.009	0.86	0.395
Functional difference (V)	225.1	4.69	<0.001	69.2	-0.546	0.302	-1.81	0.077
Taxonomic distinctness (Δ*)	2674	55.2	<0.001	60.8	-1.04	1.382	-0.75	0.456
DCA axis one (S.D.) *	16.30	0.34	<0.001	97.5	-0.376	0.025	-15.36	<0.001

Table 5-12 ANOVA results for testing the significance of regressions fitting a polynomial model to each univariate index separately with age. '*' denotes that the index values were transformed before applying regression analysis. Refer to Table 3.8 caption for an explanation of column headings.

F-test results discern which regression model statistically fits the observed index trajectory best. Therefore, indices whose trajectories are closer to a linear model are; pH, organic carbon, Simpson's evenness, functional evenness, functional difference, and taxonomic distinctness, although the degree of linearity varies among this group. The remainder; importance score, species density, Simpson's diversity, distance from lognormal, growth form diversity, functional richness, and DCA axis one have a better fit to a polynomial model, although curvature varies greatly among these indices.

A best fit result does not necessarily mean that the best fitting model is actually a significant fit, although with this data that is always the case. Also, it does not indicate

whether or not the index responds strongly to vegetation development or how consistent that response is; these properties are better discerned from studying the graphs of observed and fitted values given in Figure 5.11 (overleaf).

Index	F statistic	Fpr	Best fit model?
pH	1.31	0.261	linear
Organic Carbon % *	2.72	0.109	linear
Sample importance score (m^3_{cover})*	79.2	<0.001	polynomial
Species density (n per 100m^2)	12.1	0.001	polynomial
Simpson's diversity (-lnD)	10.0	0.003	polynomial
Simpson's evenness ($E_{1/D}$)	0.48	0.492	linear
Distance from lognormal (ΔL)	16.2	<0.001	polynomial
Shannon's growth form div. (H')	4.47	0.039	polynomial
Functional richness ($\%_{site\ trait\ range}$)	29.77	<0.001	polynomial
Functional evenness (FRO)	0.72	0.404	linear
Functional difference (V)	3.26	0.077	linear
Taxonomic distinctness (Δ*)	0.09	0.766	linear
DCA axis one (S.D.) *	236	<0.001	polynomial

Table 5-13 Results of the F-test for the null hypothesis that the polynomial regression does not fit the data better than the linear regression. '*' denotes that the index values were transformed before applying regression analyses. Rejection of the null hypothesis ($p \leq 0.05$) means that the polynomial model predicts the observed index pattern significantly better than the linear model.

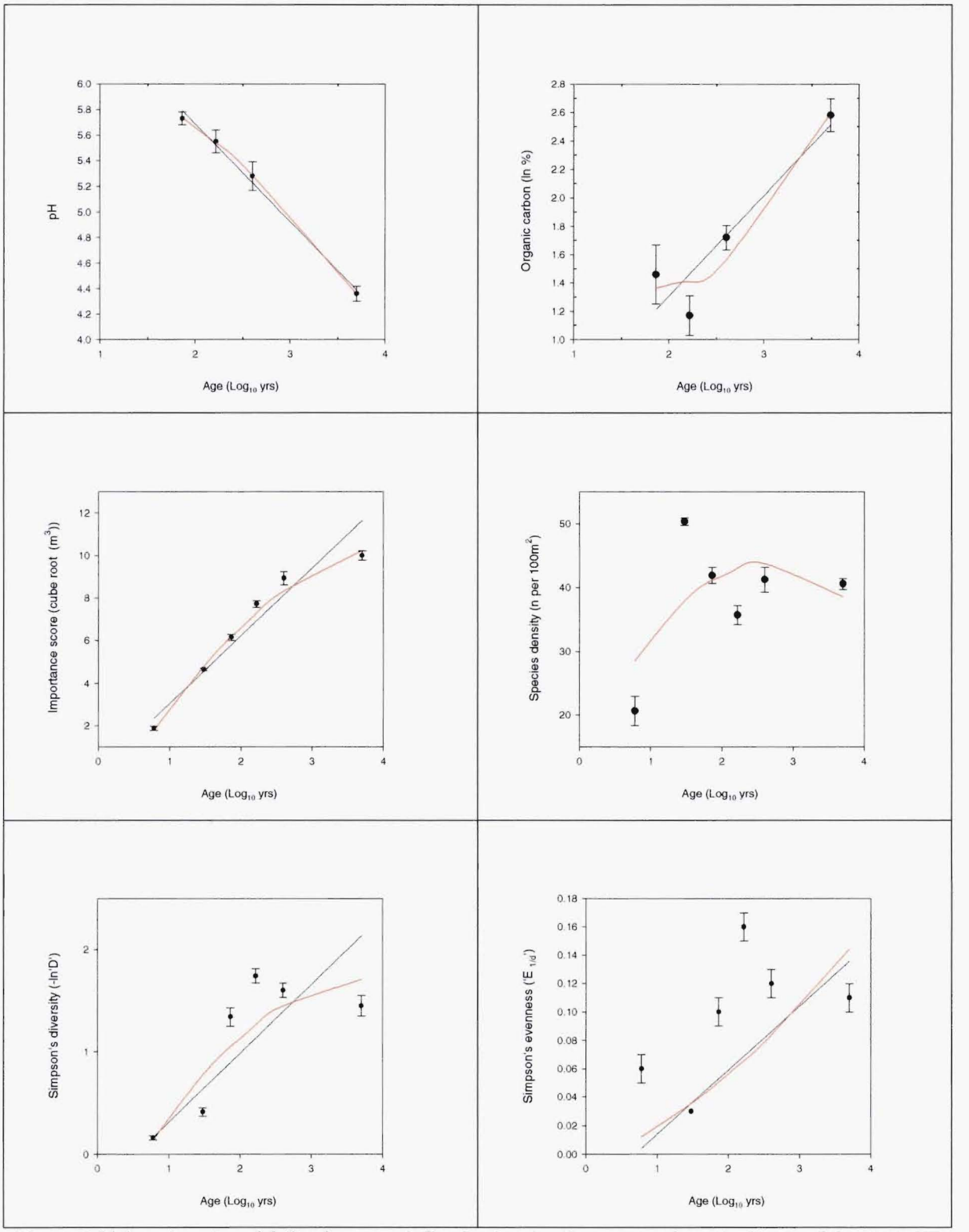

Figure 5.11 (continued on 2 following pages) Graphs showing the mean and standard error of the mean per stage for the observed data of each univariate index, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for each significant regression, regardless of whether the slope parameter was significant, or, in the case of the polynomial model whether it was a significantly better fit than the linear model.

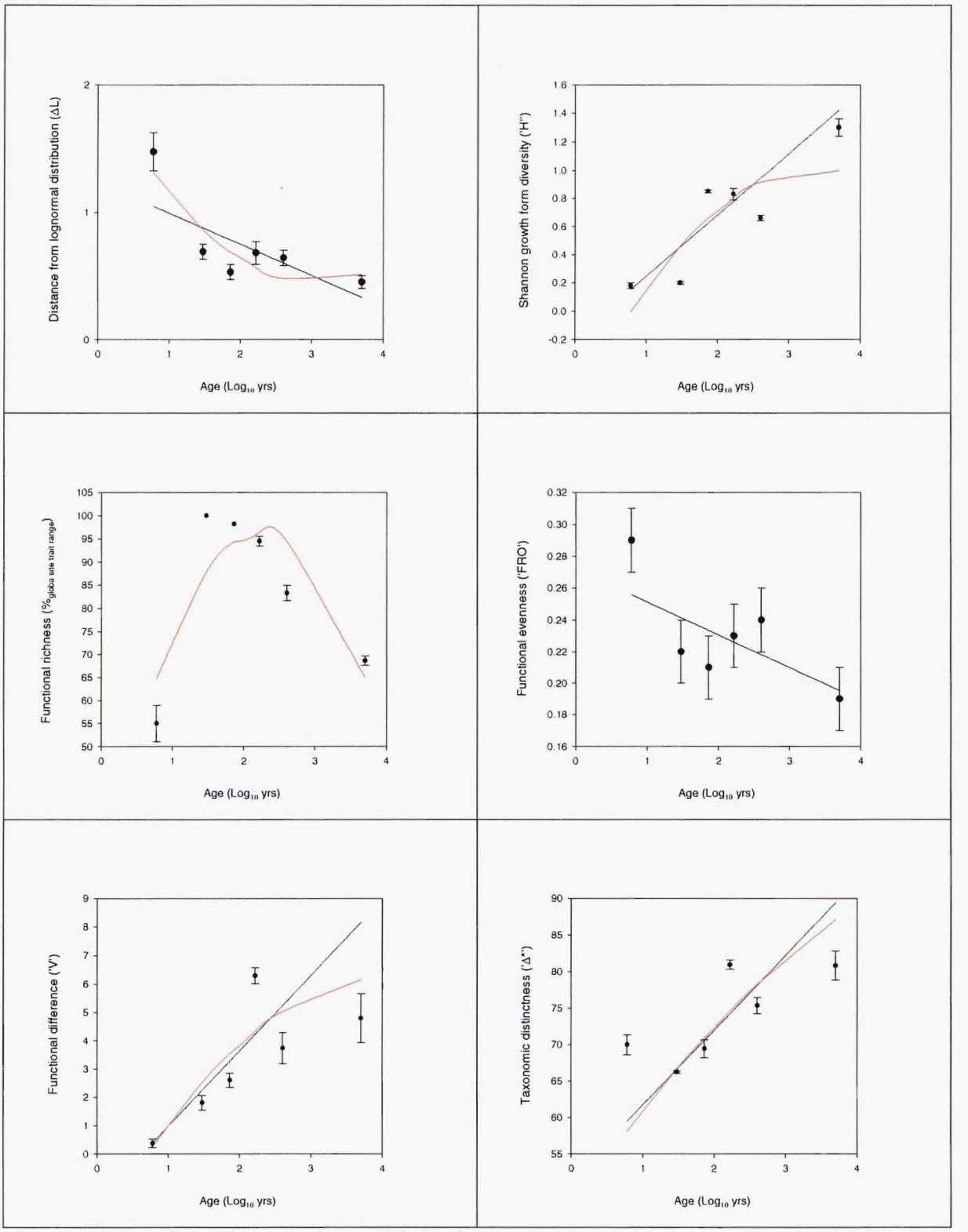

Figure 5.11 (continued from previous page) Graphs showing the mean and standard error of the mean per stage for the observed data of each univariate index, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for each significant regression, regardless of whether the slope parameter was significant, or, in the case of the polynomial model whether it was a significantly better fit than the linear model.

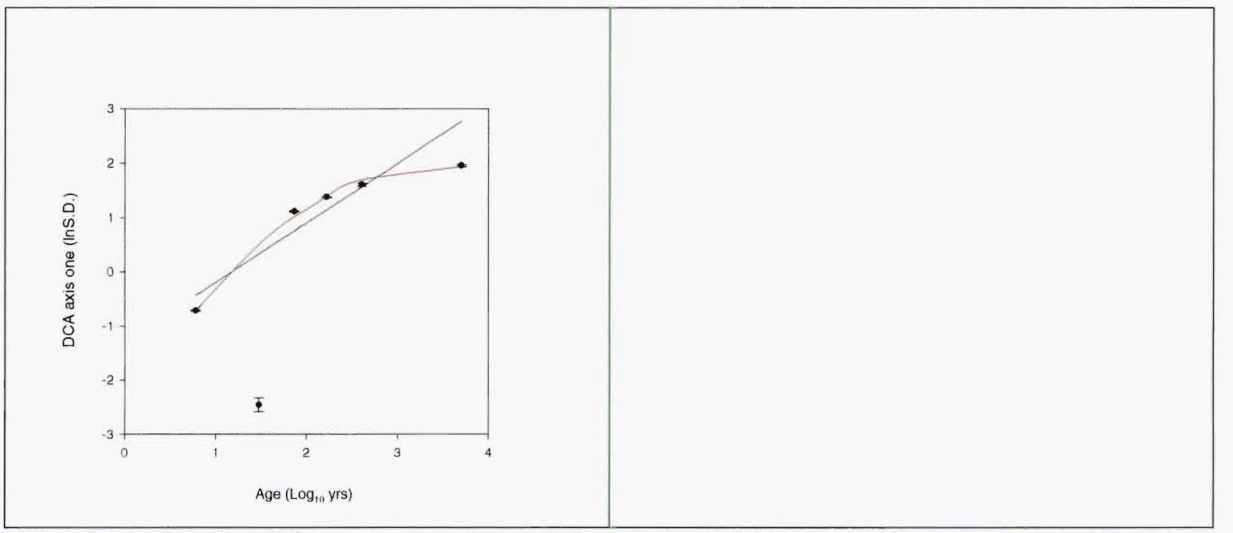

Figure 5.11 (continued from previous 2 pages) Graphs showing the mean and standard error of the mean per stage for the observed data of each univariate index, as well as the fitted lines and curves for the linear (in black) and polynomial (in red) regression models respectively. Note that fitted data is plotted for each significant regression, regardless of whether the slope parameter was significant, or, in the case of the polynomial model whether it was a significantly better fit than the linear model.

Index trajectories illustrated in Figure 5.11 are described in detail in the following sections. The sections follow the order of index appearance in Figure 5.11. By way of summary, index responses can be summarised into four categories:

1. Strong response wit a very consistent and smooth trajectory (either fitting a linear or polynomial model)
    - pH, importance score
2. Strong response with a clear trend and consistent trajectory (either fitting a linear or polynomial model)
    - Organic carbon, Simpson's diversity & evenness, distance from lognormal, growth form diversity, functional difference, taxonomic distinctness and DCA axis one.
3. Sensitive to vegetation development but with an inconsistent trajectory
    - Species density and functional richness
4. Insensitive to vegetation development
    - Functional evenness

5.4.2.6.1 Soil chemical properties

The graphs presented in Figure 5.11 show strong trends in both pH and organic carbon. The pattern of pH is a consistent and linear decrease over time. Soil organic carbon content displays a generally linear increase over time, with stage four being an outlier.

5.4.2.6.2 Importance score

There is a strong increasing trend with a consistent trajectory that levels off towards the older stages.

5.4.2.6.3 Species diversity indices

Species density

Species density does not have a consistent response to vegetation development (Figure 5.11). It increases sharply at first, followed by a decrease to a variable trajectory with no net trend. Species richness (S_{max}) also followed the same pattern (comparative results shown in Figure 5.6, section 5.3.2.3.2) emphasising that species density results truly represent variation in assemblage species richness.

Simpson's diversity

Simpson's diversity has a strong, consistent response to increasing age. The pattern is an increase followed by a levelling off in later development stages.

Simpson's evenness

Simpson's evenness has a broadly increasing trend, however the response is not particularly strong and neither is the trajectory consistent.

5.4.2.6.4 Distance from the lognormal model of species RAD

The distance from the lognormal RAD shows a strong and relatively consistent decreasing trend over time which appears to resemble an asymptotic trajectory. This provides evidence that the RAD of plant species assemblages do tend towards a lognormal pattern during recovery after ecosystem perturbation.

5.4.2.6.5 Functional diversity indices

Shannon's growth form diversity

The general trend for growth form diversity is a strong increase over time. However, the pattern is discontinuous, with almost all the increase occurring in two steps; after stage two and stage five.

Functional richness

Functional richness displayed a strong but inconsistent response to vegetation development. There was no significant directional trend over the entire gradient which may be partially due to high variance within some stages.

Functional evenness

Functional evenness broadly displays a decreasing trend over time, but the response is weak and trajectory inconsistent.

Functional difference

Functional difference displays a strong increasing response with a consistent trajectory that levels. Stage four is an outlier to the general pattern.

5.4.2.6.6 Taxonomic distinctness

Taxonomic distinctness has a strong and reasonably consistent response to the vegetation development gradient. The increasing trend is characterised by an approximately sigmoidal trajectory.

5.4.2.6.7 Species turnover - DCA axis one

Species turnover has a strong increasing response with a consistent and gradually levelling trajectory. Stage two is an outlier to the general pattern.

5.4.2.6.8 Ordination – PCA

PCA on univariate indices

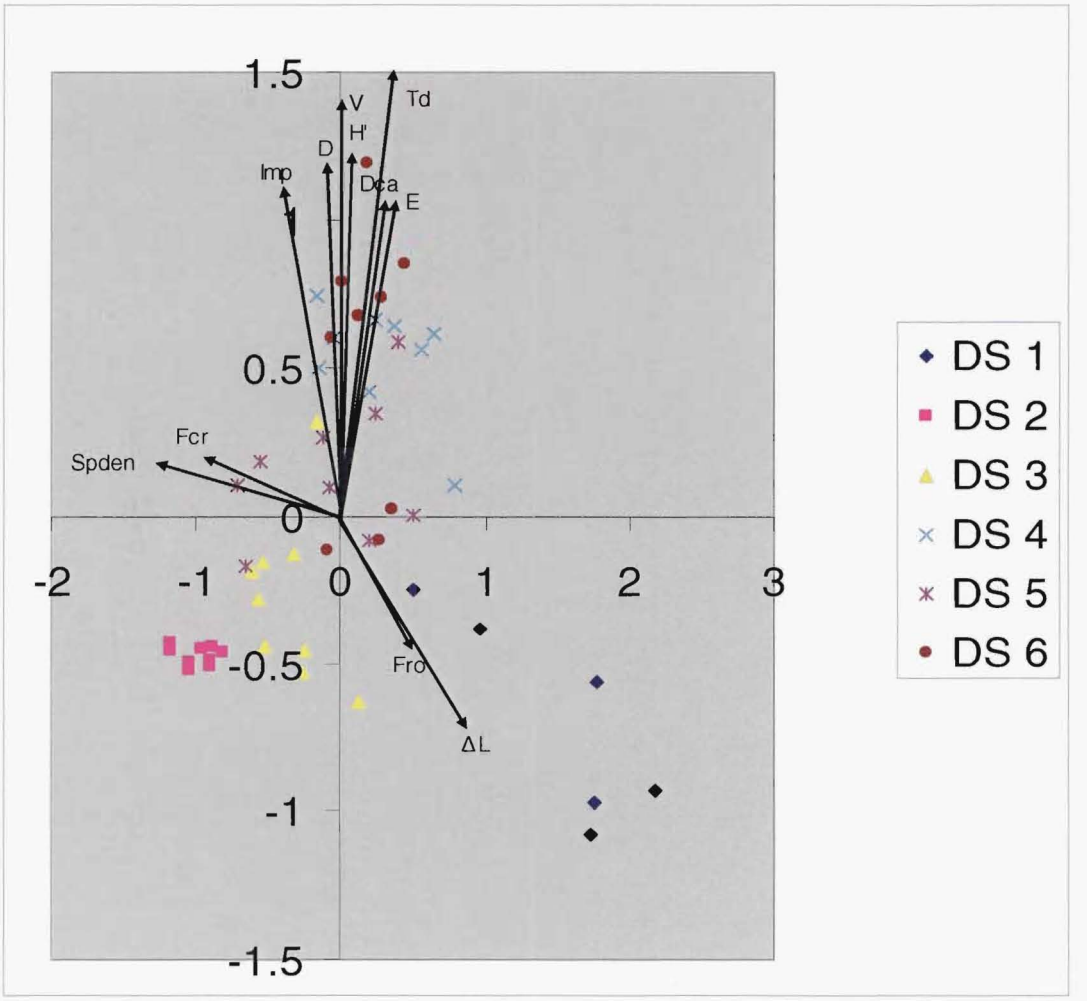

Figure 5.12 Ordination diagram of all samples based on a PCA analysis of univariate indices values. Axes one and two (shown) together comprise 86.4 % of the total variance in the species data. The eigenvalues for axes one to four are 0.579, 0.285, 0.114 & 0.013 respectively. Biplot arrows directions denote the relationships of each index to the separation of samples in the diagram, arrow length is proportional to the strength of the index's contribution to the sample variation. Key to arrows clockwise from the positive end of axis two; H' = Shannon's growth form diversity, Td = Taxonomic distinctness (Δ*), Dca = DCA axis one, E = Simpson's evenness ($E_{1/D}$), ΔL = ΔL distance form lognormal distribution, Fro = Functional evenness, Spden = Species density, Fcr = Functional richness, Imp = importance score, D = Simpson's diversity (-lnD), V = Functional difference.

Results of the indices PCA analysis illustrated in Figure 5.12 show a reasonably good separation of samples by the 11 univariate indices included in the analysis. The fact

that PCA axes one and two together comprise 86.4 % of the total variation in sample indices values means that the graph is a good summary of the analysis. Samples are grouped into development stages, however there is some overlap between DS 4, 5 & 6 groups. Because all the indices included measured assemblage structural parameters, it can be concluded that development stages are reasonably but not entirely structurally distinct. The higher degree of sample separation achieved by the DCA analysis indicates that the latter development stages are more differentiated by their assemblage composition than by their assemblage structure. However, these assemblages may not in fact be as structurally similar as this result suggests because the indices without consistent trends confound the results. Furthermore, the 11 variables (indices) in this PCA analysis do not measure all structural parameters in existence, whereas in comparison all compositional parameters (i.e. all species) are included in the DCA analysis.

The bi-plots form three distinct and well separated groups. Therefore, indices within each of the three groups of bi-plots display a high degree of inter-correlation. The degree of separation between the groups means that they have a very low correlation with each other. The degree of bi-plot correlation corresponds with relative similarity of indices response pattern to the vegetation development gradient. The three groupings are as follows: at the top; Importance score, Simpson's diversity, functional difference, Growth form diversity, Taxonomic distinctness, DCA axis one and Simpson's evenness form one large and tight group, in the middle left; species density and functional richness form another group, and finally, at the bottom right; functional evenness and distance from lognormal are together. These three groupings illustrate that there are three basic patterns of index response to age; increasing, no clear net change and decreasing respectively. However, these groupings do not indicate similarity of information encompassed by the indices within them, thus there is no implication of index redundancy within groups.

PCA of species abundance data

The first three axes of the PCA analysis depicted in Figure 5.13 account for 70.7 % of the total variation in species data. Therefore the graph trajectory is a better representation of the compositional dynamics that occurred during the vegetation development than the graph of DCA axis one and two sample score in Figure 5.8. The point of interest is to assess the complexity of the trajectory. In this case, the trajectory appears to be simple since there is no evidence of cyclic or retrogressive development.

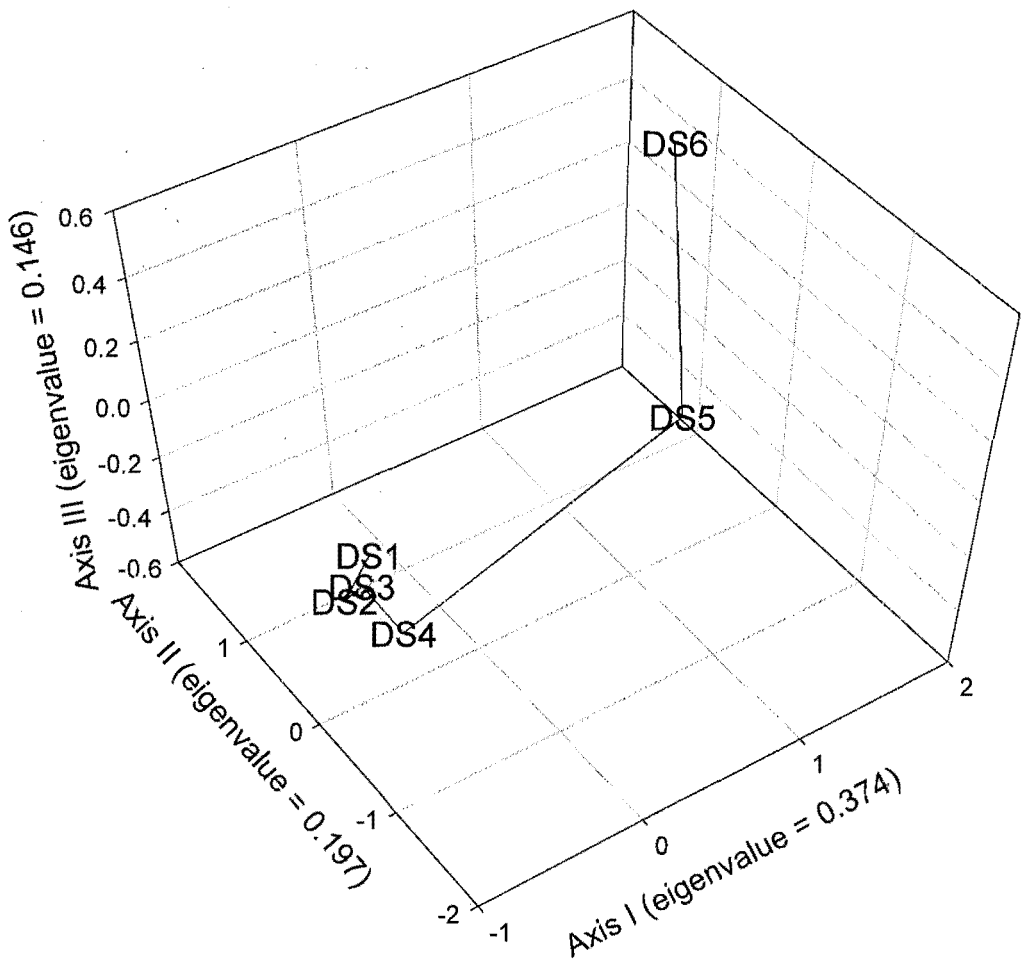

Figure 5-13 A three dimensional representation of the successional trajectory in terms of the shift in assemblage species composition. Axes values are from a PCA ordination of species abundance data.

5.5 DISCUSSION

The main objective of this chapter was to identify which indices of vegetation structure clearly track the vegetation development trajectory occurring at the Fox study site. In order to address this objective, this discussion focuses on the following questions:

- Has the chronosequence method accurately inferred the vegetation development sequence that occurred in this case?
- What successional model best describes the development sequence inferred?
- Can index performance and behaviour be explained by a combination of the following:
    - Reference to successional processes and vegetation dynamics concepts
    - Comparison to other studies of succession in deglaciated terrain

- Comparison with other index patterns from this study site

5.5.1 QUALITY OF CHRONOSEQUENCE INFERENCE

DCA and DCCA results indicate that the environmental variation existing at the site does not significantly affect the main floristic gradient. Moreover, vegetation development correlates most closely with time. The use of a variety of ageing techniques, combined with the ability to compare results with previous studies (e.g. Stevens 1968; Wardle 1973), suggests that the vegetation development trajectory has been accurately portrayed with respect to time. The floristic dissimilarity among replicate development stage samples illustrated in the DCA graph indicates that a substantial amount of the spatial heterogeneity existing within stages was sampled. Yet ANOSIM results indicate that this level of variation did not compromise the floristic distinctness of each stage. When considered together these results support the assumption that the chronosequence method is able to infer the general pattern of the vegetation development sequence that would occur at any position within the study site. Furthermore, the similarity of the composition and structural characteristics of the Fox chronosequence with others studied in the region (Wardle 1980b; Burrows 1990; Richardson et al. 2004) indicates that vegetation development in the region follows a relatively predictable trajectory, given similar initial conditions. This study does, however, provide an opportunity to study the trajectory in more detail since the sampling design is the most intensive to date, and all vascular plants have been measured for the first time.

A few features of the vegetation development warrant discussion with regard to the accuracy of the chronosequence method.

Firstly, development stage two appears to be an outlier to the general trajectory in DCA analysis. DS 2 has the lowest values of Simpson's evenness, largely owing to the dominance of *Coriaria arborea*. Yet neither DS 1 nor DS 3 have a high abundance of this species. Therefore, because sample positioning on DCA graphs is representative of the centroid(s) of dominant species within each sample, (Jongman et al. 1995) the deviation of stage two is probably owing to the abundance of *Coriaria arborea*. Wardle (1977, 1980b) associates dominance of *Coriaria arborea* in early successional stages with substrate differences. However, in this study substrate characteristics for DS 2 were not unusual, nor was their variation related to floristic heterogeneity among stage two samples. Therefore, the unusual abundance of *Coriaria arborea* is probably due to unknown historical factors such as climate variation during the establishment window among development stages

(Burrows 1995) or temporal variation in seed rain composition. Because *Coriaria arborea* inhibits growth of other species during its thicket stage (Walker et al. 2003), it would tend to dominate for a period if given the opportunity to establish, thereby accentuating the appearance of a different development trajectory taking place. Nonetheless, the low abundance of *Coriaria arborea* in DS 3 does not appear to be consistent with such a high abundance 40 years previously even if senescence is considered, although overall species composition of DS 3 appears to be consistent with a development from a DS 2 like previous state. On balance the evidence does suggest divergent trajectories occur at the Fox site during early successional stages but DCA ordination probably overemphasises this. Importantly though, Wardle's characterisation of the range of possible trajectories in the region (Wardle 1980b) suggests not only that such structural variation is within the normal range of young assemblages but also that they tend to converge towards an assemblage similar to that sampled in the later development stages of this study. Interestingly, the PCA floristics trajectory analysis did not depict stage two as an outlier, suggesting that it is a more powerful method for trajectory analysis.

A second discussion point with regard to chronosequence accuracy is that the DCCA analysis suggested that some floristic variation was due to variables not included in the DCA analysis. The obvious explanatory variables for this would be those related to substrate. However, stepwise regression analysis indicated that very little intra-stage floristic variation was due to measured substrate variables. It is concluded that this variation is probably due to either unmeasurable characteristics of the initial conditions, or, unknown historical contingency. If this is the case, at least part of this variation is associated with the type of spatial heterogeneity that would be expected to be found in a directly observed vegetation development sequence owing to chance events.

Thirdly, the DCA analysis shows variation among replicate samples to increase with age. Such a variance pattern is not observed with species density, therefore the differences between samples are likely to be in assemblage structure rather than composition. The pattern is interpreted as indicating an increase in spatial heterogeneity, rather than trajectory divergence, or, the existence of alternative trajectories. Patchiness is caused by different processes at different stages of vegetation development (Pickett & White 1985); heterogeneity in later stages is probably due to small scale disturbances, such as windthrow creating different establishment patterns. It is possible that heterogeneity itself does not increase, rather the scale of it increases concomitantly with increasing size of individuals. However, the sampling method used here cannot make this distinction.

Finally, regression analysis found a weak but significant correlation between combined sediment properties and floristics for development stage four. Field notes suggest that the greater soft sediment depth than would be accounted for by soil profile development alone at this stage is due to post formational deposition of inorganic sediment. This sediment input would also account for the low level of soil organic carbon measured in this stage. The same stage is an outlier for two other indices (functional difference and taxonomic distinctness) but the weak correlation of sediment properties with the florisitcs is unlikely to account for the magnitude of difference in the values of these indices. These differences are more likely to be due to a shift in species composition and traits associated with the presence of a forest canopy.

In summary, there is nothing in the results to suggest that the chronosequence is not sampling a single development pathway. There is evidence that the trajectory is variable, however concepts from assembly theory such as historical contingency (Noble & Slatyer 1980; Drake 1990) would suggest such trajectory band-width is to be expected. Undoubtedly, if a wider range of initial conditions and environmental variation had been sampled intensively enough, multiple pathways would have been resolved. These may be parallel, divergent, convergent or in network form. However, this study simply seeks to ensure the general trends of one development pathway have been sampled as a model of vegetation development to test indices behaviour. All results suggest that this has been done.

5.5.2 WHICH SUCCESSIONAL MODELS APPLY?

No single successional model appears to describe the vegetation development at Fox precisely. The most suitable models are relay floristics (Egler 1954) (provided the implication of discrete species assemblages is ignored) or the facilitation model of Connell & Slayter (1977). The central point of both these models is that successive assemblages 'react' (*sensu* Clements 1916) upon the site to facilitate the colonisation of the proximal assemblage.

Reaction can be inferred in every stage of the Fox sequence. For example, the mat plants of stage one would accumulate fine substrate and provide establishment sites for shrubs. Shrubs such as *Coriaria arborea* and *Carmichaelia arborea* in stage two could facilitate growth of more nutrient demanding species by fixing nitrogen. The dense tall scrub canopy in stage three probably enabled more shade tolerant species to colonise (e.g. *Weinmannia racemosa*). The more complex habitat of the low forest of stage four would

have provided diverse micro-sites for establishment of a wide array of species. Finally, the tall successional forest of stage five provides the conditions for podocarp growth. However, in reality, succession involves more than one process (including facilitation, inhibition, tolerance and competition) that would each vary spatially and temporally in their relative prominence (Burrows 1990). This picture agrees with the concept put forward by Walker & Chapin (1987) that succession is a complex of simultaneously acting processes.

Species lists provided by Reiners et al. (1971) suggest relay floristics is an appropriate model for succession at Glacier Bay also. Likewise, Veetas (1994) and Matthews (1979), from the Norwegian Bodalsbreen and Storbreen Glaciers respectively, cite evidence for relay floristics, although both authors employ other models to explain anomalies with respect to relay floristics.

5.5.3 EXPLANATION OF UNIVARIATE INDICES BEHAVIOUR

5.5.3.1.1 Soil chemical properties

The trends in soil chemical properties agree with other studies of vegetation development on deglaciated terrain, for example, at Glacier Bay, Alaska (Crocker & Major 1955), and Franz Josef Glacier, New Zealand (Stevens 1968). Data presented by Walker & del Moral (2003) for pH from eight chronosequence studies on moraines, and for organic carbon from six such studies all show the same broad pattern. Indeed, in a comprehensive review, Matthews (1992) concludes that such patterns are an almost universal feature of glacial foreland chronosequences. These patterns give insight into soil development and ecosystem functions such as decomposition. A decline in pH is linked to the accumulation of organic matter which is in turn indicative of increasing plant litter inputs and microbial activity. Interestingly, the pattern of neither soil index shows sign of levelling off within the time scale that the Fox study chronosequence spans. This agrees with Stevens' (1968) results from the neighbouring Franz Josef chronosequence. Stevens showed that a levelling of either organic carbon or pH change does not occur until beyond 5,000 years. This is associated with a mature soil profile, poor nutrient status (Richardson et al. 2004) and a higher proportion of carbon being in the plant biomass (Burrows 1990). Thus, it is reasonable to conclude that in the absence of major disturbances, soil development would continue beyond the oldest age sampled in the Fox chronosequence.

5.5.3.1.2 Importance score and DCA axis one; evidence for completion of primary succession

The increasing trend of the sample importance scores is assumed to track above-ground plant biomass accumulation following Chiarucci (1999). Such accumulation is an intuitive process of progressive succession and the approach to an asymptote observed indicates that the chronosequence sampled the development gradient until the end of primary succession. Data from the Franz-Josef chronosequnce for woody species cover percentage mirror the pattern and rate observed at Fox (Richardson et al. 2004). Other studies of deglaciated terrain mirror the general pattern of a levelling increase, although rates vary (Reiners et al. 1971; Bormann & Sidle 1990; Frenot et al. 1998; Jones & Henry 2003).

Succession is frequently characterised as the process of compositional change by species replacement (Glenn-Lewin et al. 1992); accordingly, successional rate is often measured by species turnover (Walker & del Moral 2003). Thus, DCA axis one values represent the gradient in time of vegetation development which at Fox indicates gradually levelling rates of species turnover. This is interpreted as the plant assemblage approaching a dynamic equilibrium state, marking the end of the primary succession phase. No comparison studies could be found that directly measure species turnover in deglaciated terrain, instead most studies infer species turnover from the magnitude of compositional differences. Richardson et al. (2004) found compositional change to be more gradual after 5,000 years in the Franz-Josef sequence, suggesting a similar levelling in species turnover to Fox. Burrows (1990) lends further support to this pattern by asserting that assemblages similar to the tall-forest exemplified by DS 6 at Fox can persist for many centuries in the region. Nonetheless, stability is scale dependent and species turnover would be expected to continue on a spatial scale appropriate to the disturbance regime (White & Jentsch 2001) and a temporal scale dependent on rates of environmental change (Richardson et al. 2004).

5.5.3.1.3 Growth form diversity

One mechanism by which species turnover may be stimulated is resource availability (Pickett et al. 1987b), associated with the process of mass-senescence of cohorts of successional species. The discontinuities in the pattern of growth form diversity at Fox probably reflects growth form dominance shifts resulting from such loss of some species. Indeed, Grime (2001) modelled succession in terms of shifts in growth form and other chronosequences on deglaciated terrain have inferred relatively abrupt shifts in

growth form during vegetation development (e.g. Reiners et al. 1971; Vetaas 1994). However, the arbitrary division of the vegetation development into chronosequence stages by all the empirical studies would tend to accentuate what in reality are probably more wave-like replacements into discontinuities.

5.5.3.1.4 Species density

Species density does not exhibit a consistent response to any one factor (Glenn-Lewin et al. 1992), indeed this led Whittaker (1977) to conclude that a general model of change in species density with succession would be impossible. However, the general pattern of an increase, followed by a levelling or decrease has often been inferred from chronosequences for primary plant successions with increasing terrain age, both for a variety of habitats (Walker & del Moral 2003), and in particular on deglaciated terrain (Matthews 1992). Data from the Franz Josef chronosequence (Richardson et al. 2004) agree with the basic pattern observed for Fox, although direct comparability is problematic owing to different portions of the vascular flora being measured. This problem is common for comparisons of species density among chronosequences. Nonetheless, studies on deglaciated terrain outside New Zealand suggest that response variability is considerable within this type of system. In particular, timing of the species density peak varies as well as the behaviour after the peak, with some authors reporting no decline (Reiners et al. 1971; Birks 1980; Kaufmann & Raffl 2002) and others a definite decline (Matthews 1992; Caccianiga et al. 2001). The decline is generally accounted for as a loss of species due to increasing competition for resources as vegetation cover increases (Burrows 1990).

5.5.3.1.5 Indices based on species proportional abundance

Studies employing species diversity indices (i.e. those that take into account proportional species abundances) to track succession on deglaciated terrain are uncommon. Reiners et al. (1971) found Simpson's diversity to follow a similarly pattern (of a levelling increase) to have occurred at Glacier Bay, Alaska to the one inferred at Fox, although an earlier peak suggests different rates of change. In the same study, Reiners et al. reported similar results to Fox for measures of species evenness. They found evenness not to display a consistent pattern with increasing age although the general trend was an increase. Comparison of the patterns of species density, diversity and evenness at Fox suggests that the incorporation of species density into measurements of the equity of proportional

abundances (i.e. evenness) dampens the oscillations of evenness about the general pattern of change with age.

The general trend of increasing evenness is reflected in the trend for decreasing distance from lognormal. Ecological interpretation of these trends relates to a tendency for greater equity in niche apportionment as ecosystems develop (Tokeshi 1993). However, proximity to the lognormal distribution implies that a small number of species retain a greater proportion of the resources, hence the levels of evenness attained in the later development stages is still far from total equity. Whereas no examples of RAD analysis *per se* could be found in studies of deglaciated terrain succession, reports of a general increase in evenness of species abundances (Reiners et al. 1971; Matthews 1992) would suggest a tendency towards the lognormal pattern.

No comparative work conducted in deglaciated terrain could be found for either distance from lognormal, all four functional diversity indices or taxonomic diversity. Inferential comparisons have been made for growth form diversity and distance from lognormal. The remaining four indices can be interpreted from knowledge of the species assemblages they measure.

5.5.3.1.6 Functional diversity indices and taxonomic distinctness

The pattern of functional richness is similar to species density and the two are probably related. This is because as species numbers increase, so too does the probability that a wider range of leaf morphology will be present in the assemblage. The decrease in functional richness in later stages is however more marked than that for species density. This is possibly because leaf morphology is related to life-strategy and the highly competitive environment of later stages does not allow for the presence of many ruderal species that in Fox tend to have larger leaves.

The increase in functional difference is possibly related to the increased evenness of species abundance (Simpson's evenness). This effectively spreads out the distribution of abundance within the range of leaf forms present within each stage; this spread is what functional difference measures. The two indices do share roughly the same pattern of variation.

Taxonomic distinctness does not appear to be closely related to any other index; this would support its creators' assertion that it contains different information to other diversity indices (Clarke & Warwick 1998). Certainly, it is unrelated to species density since stage two is the lowest value for taxonomic distinctness yet is the highest for species

density. The fact that the pattern is the same as functional difference except for stage one is interesting because Petchey and Gaston (2002) noted that functional and taxonomic diversity are sometimes correlated. This correlation is intuitive because a greater taxonomic spread is likely to result in a greater spread of functional traits since niche type is related to life history attributes which are in turn correlated with taxonomic relatedness. A possible reason for the increase in the taxonomic distinctness among species along the development gradient is that the gradual increase in habitat structural diversity provides a greater diversity of niches.

Finally, the response of functional evenness is too weak and the pattern too varied to attach any valid interpretation.

5.6 CONCLUSION

In summary the chronosequence studied at Fox Glacier provides a robust inference of the general pattern of vegetation development that occurs under contemporary environmental conditions. As such it is suitable to use as an analogue model of primary succession at a restoration site. The long gradient of vegetation development combined with relatively low levels of spatial heterogeneity facilitates the resolution of index response patterns. Many of the indices show a strong response and some of these are consistent enough to be able to evaluate progress of ecosystem development. The next chapter provides a synthesis of index behaviour among sites to establish if their consistency is dependent on the specific characteristics of different plant assemblages or not.

6 COMPARISON OF INDICES RESPONSE TO VEGETATION DEVELOPMENT AMONG STUDY SITES: A SEARCH FOR PREDICTABLE & COMMON BEHAVIOUR.

6.1 OVERVIEW

The aim of this chapter is to identify which indices have predictable enough responses to the different vegetation development gradients previously described in order to be potentially useful evaluators of restoration success for distant goals using the trajectory analysis evaluation strategy. There are two objectives of this chapter. Firstly to examine which indices have predictable responses to the vegetation development gradients inferred from each site, and within the predictable subset which indices have similar trend directions among sites. The second objective is to offer a brief explanation for the observed index responses.

Index response predictability among sites is assessed semi-quantitatively by a combination of reviewing fitted regression results detailed in Chapters three to five and examining the observed response pattern of each index. A sequential regression method for quantitatively assessing similarity of index trajectories among sites is trialled but rejected in favour of visual comparison of normalised curves to simply assess similarity of trend direction among sites. From these assessments, the indices are categorised into three response behaviour categories; predictable with a universal trend direction, predictable with different trend directions and unpredictable. Of the thirteen indices tested a total of eight were found to be predictable among sites, the remainder being unpredictable. Of the predictable indices, four had similar trends among all sites (pH, organic carbon, importance score and DCA axis one) and four had predictable but different trends among all sites (Simpson's diversity, distance from the lognormal RAD, Shannon's growth form diversity & taxonomic distinctness). In the discussion section, an ecological reasoning for each behaviour category is presented based on the linkage of the indices concerned with the process of succession, ecosystem function and plant assemblage structure and composition.

This chapter seeks to address thesis question III, as set out in the general introduction:

Which indices have strong and consistent responses to all three case study vegetation development gradients; i.e. which of the tested indices have predictable enough responses to be suitable for the evaluation of restoration success via trajectory analysis?

6.2 INTRODUCTION

Studies of successional sequences have been commonplace throughout the history of ecology, but comparative studies that analyse several sequences with the same methodology are rare (Walker & del Moral 2003). Such comparative studies are valuable to search for generalities in the way that the structure of different assemblages forms, as well as to investigate linkages between ecosystem attributes. Furthermore, identifying general patterns of structural dynamics among distinct ecosystems is a key step towards developing the trajectory analysis strategy of evaluating restoration success.

Chapters three to five of this thesis have applied the same methods to investigate change in structure and composition of vascular plant assemblages as well as soil chemical properties during primary succession in three distinct ecosystems. The current environment, environmental history (Trewick & Wallis 2001) and disturbance regime are different among the three sites. Environmental differences include altitude, rainfall, temperature regime, dispersal barriers, soil type, drainage and substrate. Thus, filtering effects (Whisenant 1999) mean that the three systems have different species pools from which assembly can take place, although the relative proximity of the sites means that many generalist and some specialist species are in common, at least at some stage. Intuitively, the two forest systems would seem likely have similar structural properties because of similar growth forms and vegetation stature, nevertheless life-histories of the dominant species in the final stages are dissimilar. Thus they have quite different assemblage structural dynamics. The grassland ecosystem has obvious differences in the growth form, life-history and size of its constituent species compared to those of the forest systems. Yet some structural patterns are very similar to one or other of the forest systems. Differential species performance as a result of resource availability, plant ecophysiology and life history means that the time to complete the primary succession process is quite different among sites.

6.3 METHODS

6.3.1 DEFINING PREDICTABLE BEHAVIOUR

6.3.1.1 Historic consideration of restoration evaluation parameter predictability

No specific guidance could be found in the restoration ecology literature regarding minimum predictability thresholds for indices of vegetation development to be considered useful for trajectory analysis evaluation. This lack of rigour is reflected in the definition of trajectory analysis published by the Society for Ecological Restoration International: "...trends that lead towards the reference condition confirm that the restoration is following its intended trajectory" (SER Science and Policy Working Group 2004, p 9). The most closely related guidance is limited to comments about what properties of the reference assemblage are desirable yet not immediately restorable and can be easily measured (e.g. Westman 1991; Hobbs & Norton 1996; Ehrenfeld & Toth 1997). Perhaps because trajectory analysis *per se* is not standard evaluation protocol, measures are often used to give an impression of how disparate the restoration and reference sites are without knowledge of, or at least without relation to, their recovery trajectories (e.g. Findlay et al. 2002; Longcore 2003). In my view, this approach is a major flaw of current restoration success evaluation practice. For example, species richness is possibly the most commonly used measure of restoration success, yet the succession literature is littered with examples of its unpredictable response to development gradients (Glenn-Lewin et al. 1992; Bazzaz 1996).

6.3.1.2 The definition of index response predictability developed in this study

In view of the historic paucity of attempts to develop the trajectory analysis strategy an original attempt is made in this chapter to define the properties of an index response to a vegetation development gradient that represents a minimum level of predictability for effective trajectory analysis. This definition is designed to be independent of the limited array of indices and development gradients that this thesis has been able to provide for predictability testing.

Ideal predictable behaviour of an index would perhaps be a perfectly linear relationship with any gradient of vegetation development, provided the use of complex modelling procedures is assumed not to be practical. Since rates of development tend to slow towards the end of any development gradient (Odum 1969; Ricklefs 1973; May 1976; Glenn-Lewin et al. 1992; Elton 2000) such a relationship when plotted against time would

tend towards an asymptotic curve. Many of the indices in this study behaved approximately in this way for at least one site. However, an index conforming to an asymptotic trajectory in all sites was exceptional. This is unsurprising since some trajectory irregularity would be expected owing to the combined effects of vegetation dynamics complexities (Drake et al. 2001b; Young et al. 2001) and the potential inaccuracies of dynamics inferral by means of chronosequences (Pickett 1989). Therefore, if a range of indices are to be considered predictable, clearly a realistic definition of predictability that is inclusive of some trajectory irregularity is desirable.

In this thesis, a realistic definition of predictable is derived by postulating the minimum level of predictability required for an index to be useful for restoration evaluation by trajectory analysis. It is considered necessary that a minimum level of index response predictability should be sufficient to allow a dual facility. Firstly, it should enable the direction of the future trajectory to be estimated. Secondly, it should afford confidence that the level of recovery recorded is not an anomaly and will be sustained. Hypothetically, this minimum level would translate to index responses to different vegetation development gradients always being strong with a clear unidirectional trend and limited trajectory irregularity (i.e. a 'consistent' trajectory *sensu* term definitions in section 1.6). Some trajectory irregularity should not prevent the use of an index for trajectory analysis, as long as its amplitude is small relative to the trend. Also a larger amplitude of contra-trend response would be allowable if it occurred during the final part of the trajectory because this would be well beyond the timescale of evaluation measurements considering the time-span of the case study chronosequences.

Cases of indices being both predictable and having the same trend direction among sites are of interest because such indices have potential to be generically applicable regardless of composition and structural identity of the system being evaluated, and therefore, without the need for reference information. These cases are considered to equate to a higher level of predictability.

Cases of indices having the same trajectory shape in addition to being predictable and having the same trend direction among sites are of minor interest. This is because having the same trajectory shape would only allow a slightly higher degree of confidence than having the same trend in terms of any estimates made of future states owing to the length of development gradient that would normally exist between the state at the time of evaluation and the reference state. Thus, these cases are not considered to correspond to a higher still level of predictability.

6.3.2 IDENTIFYING PREDICTABLE RESPONSES

A mix of quantitative, semi-quantitative and qualitative methods were used to answer the three questions detailed in Figure 6.1. The output of this chapter stems from the first two questions (contained within the upper box) and is a three tier classification system for indices in terms of their proposed utility for the trajectory analysis method of ecological restoration evaluation. This categorisation exercise enables the separation of the sub-set of indices that are discussed in the final chapter. The third question in Figure 6.1 is of interest but does not confer an additional tier in the utility classification; hence it is positioned separately (in the lower box).

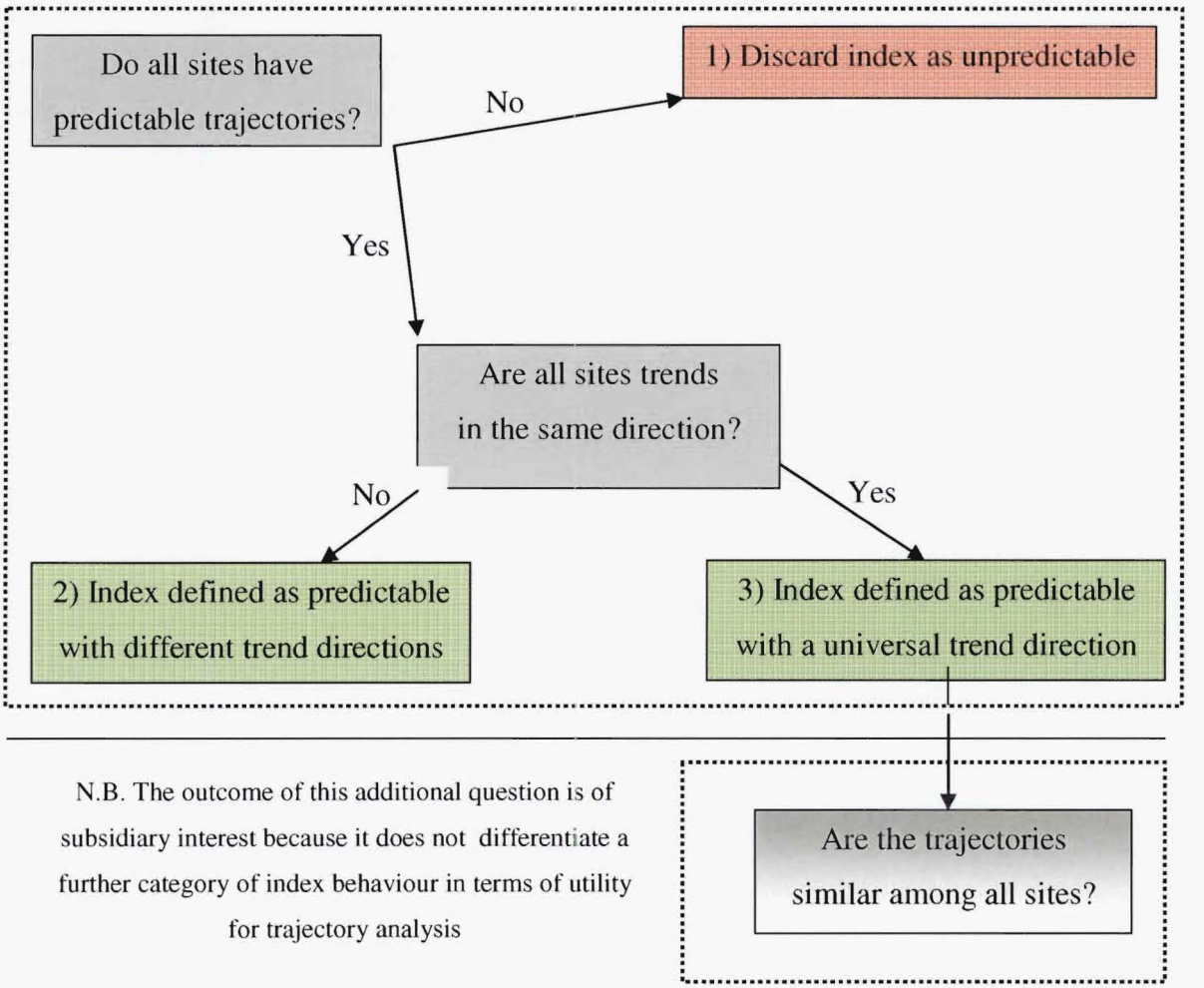

Figure 6.1 A flow chart representing the decision making process undertaken to classify the indices in terms of their common response behaviour to vegetation development gradients. The upper section is actively used; shaded boxes correspond with methods for differentiating index categories and un-shaded boxes correspond with the three output categories. The lower section did not produce an output category.

6.3.2.1 Identifying indices with predictable responses among sites

This section covers the first question box in Figure 6.1. As discussed above, for purposes of this thesis, 'predictable' is defined as 'a strong response and clear directional trend.....with limited trajectory irregularity'. Therefore, to screen indices for predictability one must check that the response for each site meets all of the three quantitative and semi-quantitative criteria listed below.

1. A very significant linear regression result (Fpr $\leq$0.01); this indicates a significant directional trend over the entire vegetation development gradient.
2. A consistent trajectory, defined as there being a maximum of one outlier to a uni-directional trend in the observed data. An outlier was defined as a data point which forces a section of the trajectory formed from joining development stage mean values to be in an opposite direction to the general trend (provided that the deviation is of high enough amplitude for the y-axis value range of the standard error bars of the outlier value and both of its neighbouring mean values not to be overlapping).
3. The best fitting regression model to the observed data had to be either linear, or polynomial with a low curvature. Acceptable levels of curvature are either an asymptotic trajectory or a trajectory which reaches an asymptote and then has a limited reversal between the final development stages only.

Using these criteria to identify predictable behaviour involved comparing the linear regression results tables as well as the graphs of observed and fitted results presented in the regression part two sections of Chapters three, four and five. Firstly, the linear regression results tables were checked for a very significant result. Secondly, the observed results were screened for outliers. Lastly, curvature of the best fitting regression model was assessed. All those not considered to be predictable were classified as unpredictable. For clarity, comparative summary graphs showing observed results for all sites and fitted results for all sites for which the index concerned was predictable are presented in Figure 6.2.

6.3.2.2 Identifying indices with similar trend directions among sites

Following on from the assessment of predictability, all predictable indices were assessed for trend direction similarity or dissimilarity among sites; corresponding to the second question box in Figure 6.1. This was done by checking the graphs in Figure 6.2 that compare site trajectories for each index individually.

6.3.2.3 Identifying indices with similar trajectories among all sites

As depicted in Figure 6.1, trajectory similarity among all sites of each index was assessed despite the outcome being of no consequence to the predictability category that the index was classified as. The methods are described and results are presented for completeness and, furthermore, because it is recognised that as the field of trajectory analysis advances appropriate methods of pattern recognition will need developing. Two methods of assessing similarity are described. A quantitative method based on regression was trialled but rejected as unsuitable. Regression was unsuitable owing to a combination of its stringency and time-scale differences between the data sets; the results section describes these problems in more detail. The qualitative method of normalising the y-axis values among sites adopted is arguably not stringent enough but appears to be more suitable.

6.3.2.3.1 Sequential regression

The regression methods used to assess statistical similarity of individual index trajectories among sites are unique to this chapter, so are fully detailed herein rather than being covered in the general methods, Chapter two. The method involved building a regression model for each index individually, through fitting five terms sequentially. Exactly the same method was applied to each index; the process was as follows:

1. the factor 'site' was fitted; a significant regression[1] meant that the overall mean value (unadjusted for age) differed significantly between sites.
2. the linear contrast in the variable log(age) was added to the model; a significant regression meant that the average slope of the index among sites was significantly different to zero slope; i.e. there is some trend with age that was common among sites.
3. the linear contrast in the variable log(age) was fitted separately for each site; a significant regression was interpreted as there being significantly different

[1] In all cases for all five terms in the regression procedure, the critical value for significance was $p \leq 0.05$.

slopes (i.e. different strengths of response and/or trajectory direction) among sites.

4. the variable log(age) was fitted with the same second order polynomial (quadratic) model for all sites; a significant regression in this case meant that there was a common curvature for all sites over and above any linear slopes.
5. the variable log(age) was fitted with a separate second order polynomial model for each site; a significant regression was interpreted as there being significantly different curves (i.e. non-linear trajectories of change) among sites.

In summary, to assess trajectory similarity, the key results to be scrutinised were the regression significance p-values ('Fpr' results) from the third and final terms in the regression modelling sequence described above. One interpretation of a non-significant result for these terms is that the sites may share a statistically similar trajectory for the particular index in question. Specifically, a non-significant result for term three or five translates to all sites trajectories fitting either a common linear or common polynomial model of change respectively.

Data manipulation

In all runs of the regression procedure, the same outlier samples were removed from the analysis as were removed for the regressions performed to test age dependency of each index for each site (details in regression methods sections of Chapters three, four, & five). Only those indices that required transforming for all sites individually (importance score and organic carbon) were transformed for these analyses. The same weightings used to reduce the effect of heteroscedasticity among stages of each index per site were used for this analysis.

6.3.2.3.2 Comparison of normalised curves by eye

To facilitate the assessment of trajectory similarity through comparisons of response curves by eye, the y-axis data was normalised onto an equivalent scale. Normalisation was achieved by transforming each development stage mean value to be a proportion of the maximum value the index attained for each site.

6.4 RESULTS

6.4.1 IDENTIFYING PREDICTABLE RESPONSES

The results section of this chapter follows the order of the methods section. The first two sub-sections correspond to the results of the questions in the upper part of Figure 6.1. These form a brief assessment of index response trajectories that supports their classification into the three categories detailed in Table 6.2 at the end of the results section. The terminology used in the descriptions of index responses in the results and discussion sections are fully defined in section 1.6 (general introduction) for clarity.

6.4.1.1 Identifying indices with predictable responses among sites

The graphs in Figure 6.2 provide a convenient reference that illustrates predictable index behaviour; for each index, best fit regression model data is plotted only for those sites where its response was considered to be predictable. Thus, the indices which were classified as being predictable in Table 6.2 have regression fit data plotted in Figure 6.2 for all study sites where the index was measured. Those indices defined as predictable were; pH, organic carbon, importance score, Simpson's diversity, Shannon's growth form diversity, distance from the lognormal RAD, taxonomic distinctness and DCA axis one. All these indices defined as predictable actually had highly significant regressions ($p \leq 0.001$, 'fpr' results), except for organic carbon at the Thomson site, for which the p-value was 0.003. This result represents a higher level of significance than the threshold that was set in section 6.3.2.1 ($p \leq 0.01$) and indicates that the second criterion identified in section 6.3.2.1 (that which relates to levels of trajectory irregularity) increases the rigour of the definition of predictability despite being semi-quantitative.

The remaining five indices were classified as unpredictable; species density, Simpson's evenness and functional richness/evenness/difference. All these indices failed the first criterion for predictability (by having insignificant linear trends) except for functional difference from the Godley site and Simpson's evenness from the Fox site. However, in both these cases they were not highly significant and the coefficients of determination for the linear regression were low (<15 %), indicating highly inconsistent trajectories. Insignificant trends appeared to be most commonly due to highly inconsistent trajectories (e.g. species density/functional difference). Whereas in one case (functional evenness), the index was simply insensitive to two of the vegetation development gradients.

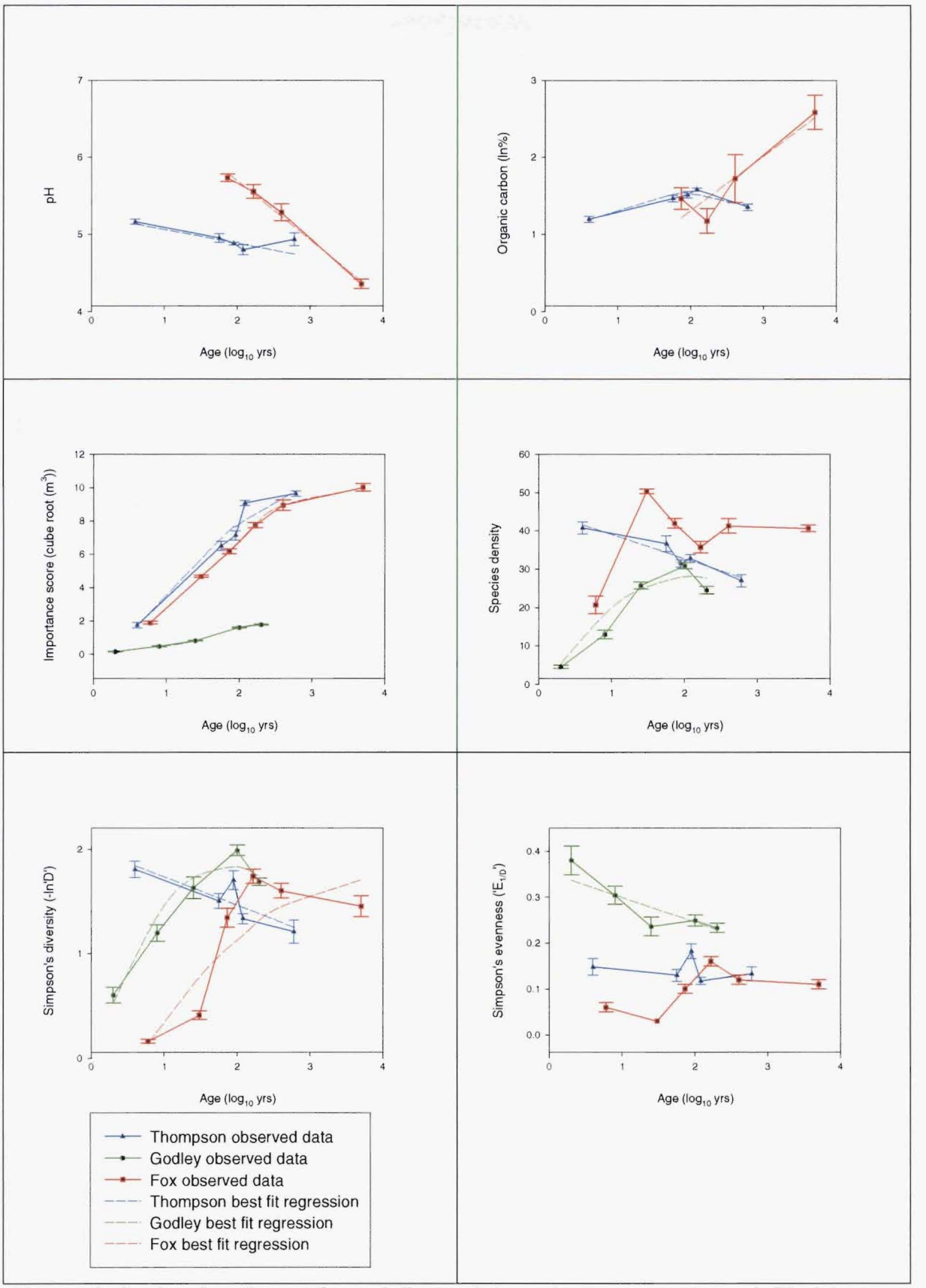

Figure 6.2 (Continued on the next 2 pages) Graphs of observed index response (mean & SE of the mean per stage) for all indices and sites. Best fit regression models are shown for those indices considered to have a predictable trajectory (see section 6.3.2.1).

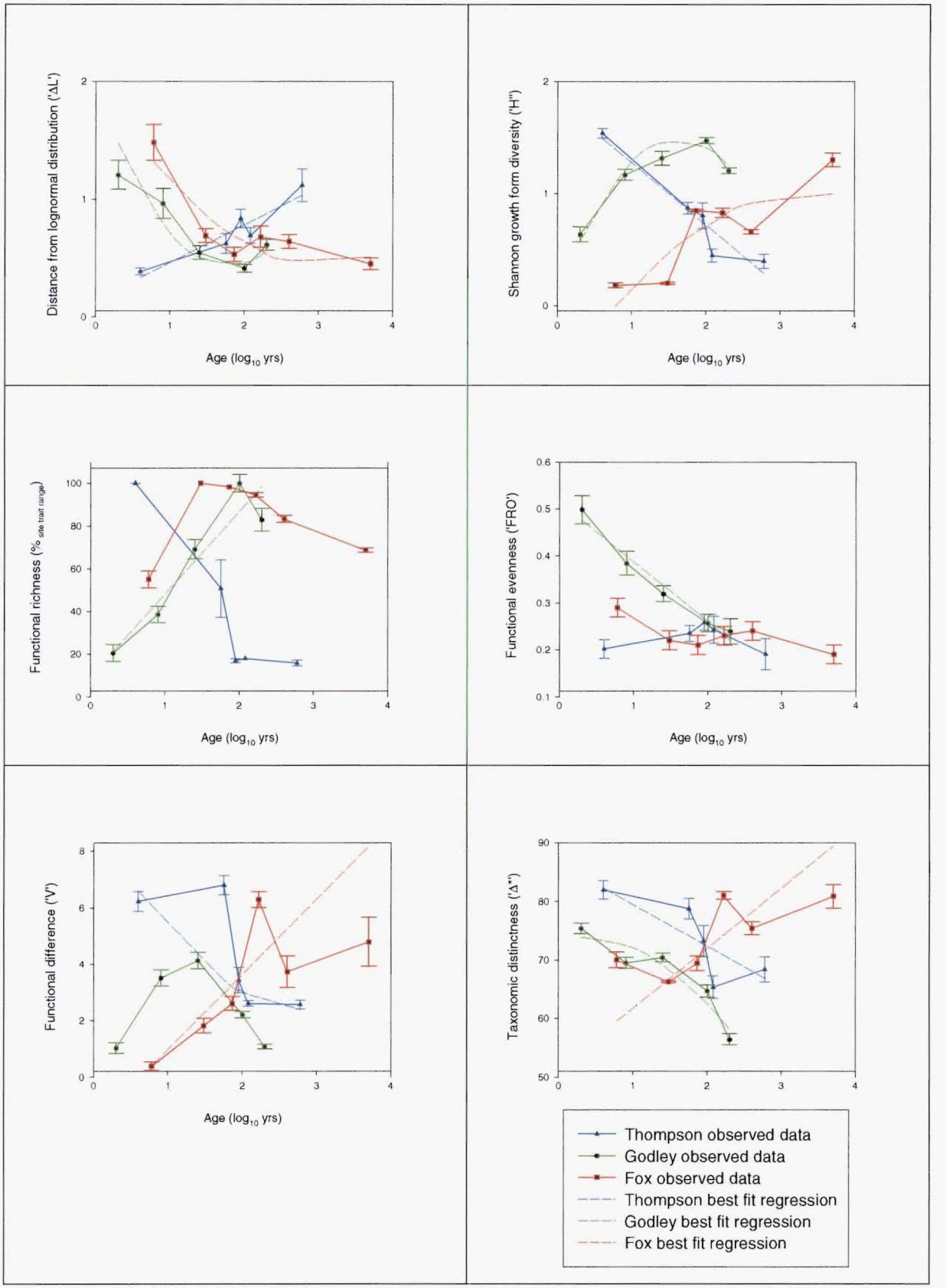

Figure 6.2 (continued from previous page) Graphs of observed index response (mean & SE of the mean per stage) for all indices and sites. Best fit regression models are shown for those indices considered to have a predictable trajectory (see section 6.3.2.1)

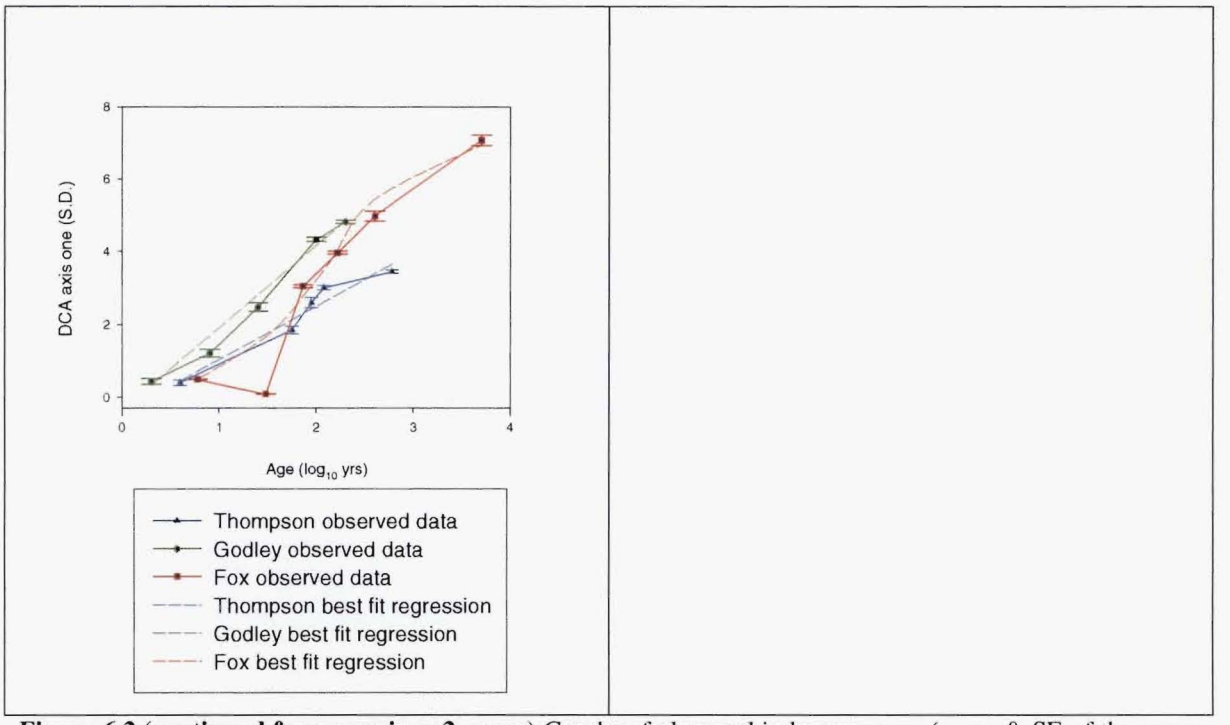

Figure 6.2 (continued from previous 2 pages) Graphs of observed index response (mean & SE of the mean per stage) for all indices and sites. Best fit regression models are shown for those indices considered to have a predictable trajectory (see section 6.3.2.1).

6.4.1.2 Identifying indices with similar trend directions among sites

From assessing the graphs in Figure 6.2, four of the indices listed in section 6.4.1.1 as predictable were deemed, in addition, to share a similar trend direction among sites. These were; pH, organic carbon, importance score and DCA axis one.

6.4.1.3 Identifying indices with similar trajectories among all sites

Results from this section do not resolve an additional level of predictability beyond the two identified by the previous two sections.

6.4.1.3.1 Sequential regression

Table 6.1 summarises the results of the regression procedure designed to establish similarity of indices trajectories among sites.

All sites sequential regression comparison				
Index	**Linear fpr**	**Similar linear trajectory?**	**Polynomial fpr**	**Similar polynomial trajectory?**
pH	<0.001	N	0.03	N
Organic Carbon (ln %)	<0.001	N	<0.001	N
Importance score (cube root m^3_{cover})	<0.001	N	<0.001	N
Species density (n per sample)	<0.001	N	0.006	N
Simpson's dominance (-lnD)	<0.001	N	0.026	N
Simpson's evenness ($E_{1/D}$)	<0.001	N	0.003	N
Distance from lognormal (ΔL)	<0.001	N	0.008	N
Shannon's growth form div. (H')	<0.001	N	<0.001	N
Functional richness ($\%_{site\ trait\ range}$)	<0.001	N	<0.001	N
Functional evenness (FRO)	<0.001	N	0.069	Y
Functional diversity (V)	<0.001	N	<0.001	N
Taxonomic distinctness (Δ*)	<0.001	N	0.003	N
DCA axis one (S.D.)	<0.001	N	<0.001	N

Table 6-1 Summary table of the sequential regression results to ascertain similarity of indices trajectory among the three sites in this study. The critical value for proof of statistical similarity is $p \geq 0.05$.

Results in Table 6.1. indicate that the only index which has a statistically similar trajectory among all sites is functional evenness, when fitted to a polynomial model. This result, as well as those indicating that importance score and DCA axis one did not have statistically similar trajectories, were not expected on the basis of the similarities apparent in the comparative graphs in Figure 6.2. Therefore, the detailed results (ANOVA tables in Appendix ten and un-presented default GenStat regression output graphs) were assessed to establish the cause of the apparent anomaly. In the case of functional evenness, a high ratio of residual mean square to total mean square exists (Appendix ten), resulting from the relatively high variation about the mean compared to the response of the index. This meant that whilst fitted polynomial curves with separate parameters were in fact different shapes to each other, there was no statistical difference between this scenario and the common parameter polynomial fit scenario. In the case of DCA axis one and importance score, the mean squared results in the ANOVA tables (Appendix ten) show that the separate parameter polynomial model did fit quite well compared to the common parameter polynomial model. These results would appear to support trajectory similarity, yet there was a statistically significant difference between the fits. Examination of the graphs in Figure 6.2 reveals that in both indices cases the only major difference between the sites

likely to have caused a statistical difference in trajectories was that the slope of one site was quite different to the others. In the case of importance score, the Godley site was the odd one out; for DCA axis one, it was the Thomson site that was different.

Flaws in regression methods for assessment of trajectory similarity

As the discussion in the previous paragraphs implies, there are problems with this method regarding its ability to resolve similarities in trajectory shape among indices with these data sets. Firstly, GenStat automatically extrapolated the slope parameters for each site in order to extend the fits of each site to cover the total age range of all sites. This acts to bias the results; either masking or falsely enhancing similarity of observed trajectories. Secondly, even if it is assumed that this bias is not active, the statistical definition of trajectory similarity prescribed by this method appears to be unnecessarily stringent for the purposes of this study. For example, for trajectories to be statistically dissimilar requires only a small drop in the regression mean squares (proportionally to the residual mean square) upon the fitting of linear or polynomial models with different parameters for each site. Moreover, a non-significant result for step 3 or 5 (i.e. statistically similar trajectories) actually represents a similarity in both slope and shape, whereas slope is not a relevant facet of trajectory similarity, since rate is not of specific interest to trajectory analysis as defined in this thesis.

Thus, as a consequence of these issues with the regression methodology it is considered that the results may be misleading. For example, some indices with ostensibly quite similar trajectories may not have statistically similar trajectories. Conversely, it is also possible that those with statistically similar trajectories do not actually have the most similar trajectory patterns. Whereas the resolving ability of the regression procedure could theoretically be much improved if each site's data was adjusted to a normalised time scale, this was not attempted because further development of methods for the assessment of statistical similarity was decided to be not worth the effort. This conclusion was reached for two reasons. Firstly, less quantitative methods were deemed to be sufficient for the

purposes of investigating the thesis questions pertaining to index trajectories[2]. Secondly, in restoration evaluation by trajectory analysis no use could be envisaged for such a method. The reasoning for this being that the assessment of whether a trajectory is likely to continue towards a goal would not normally rely on comparison of trajectories since knowledge of a reference recovery trajectory for the parameter of interest would be rare.

6.4.1.3.2 Comparison of normalised curves by eye

Figure 6.3 contains comparative graphs of all indices trajectories among sites with the y-axes on a normalised scale to facilitate comparison of trajectories by eye. The only index that appeared to have a similar trajectory throughout the entire development gradient from assessing these graphs was importance score. DCA axis one had fairly similar trajectories among sites. However, the inconsistency of DS 2 at the Fox site prevents this index from being defined as having a universal trajectory.

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[2]Question III: *Which indices have strong and consistent responses to all three case study vegetation development gradients; i.e. which of the tested indices have predictable enough responses to be suitable for the evaluation of restoration success via trajectory analysis?* Question IV: *Which type of restoration goals are the indices suitable for trajectory analysis able to evaluate?*

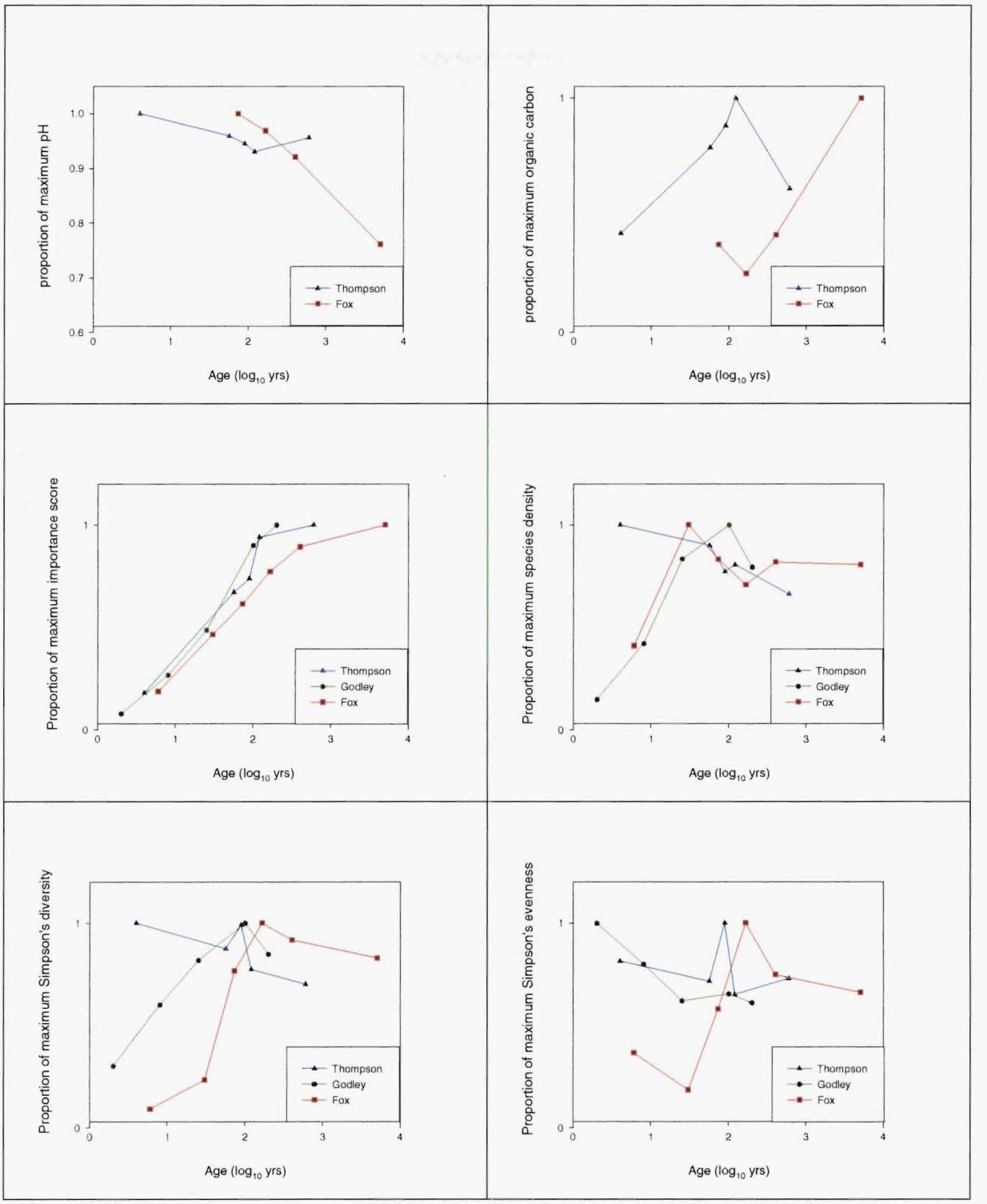


Figure 6.3 (continued on next two pages) Normalised graphs to compare indices trajectories on the same y axis scale in order to aid visual comparison of the trajectories. The mean values for each stage (same outlier samples removed as for regression analysis) of each site are normalised by converting them to a proportion of the maximum value for that site.

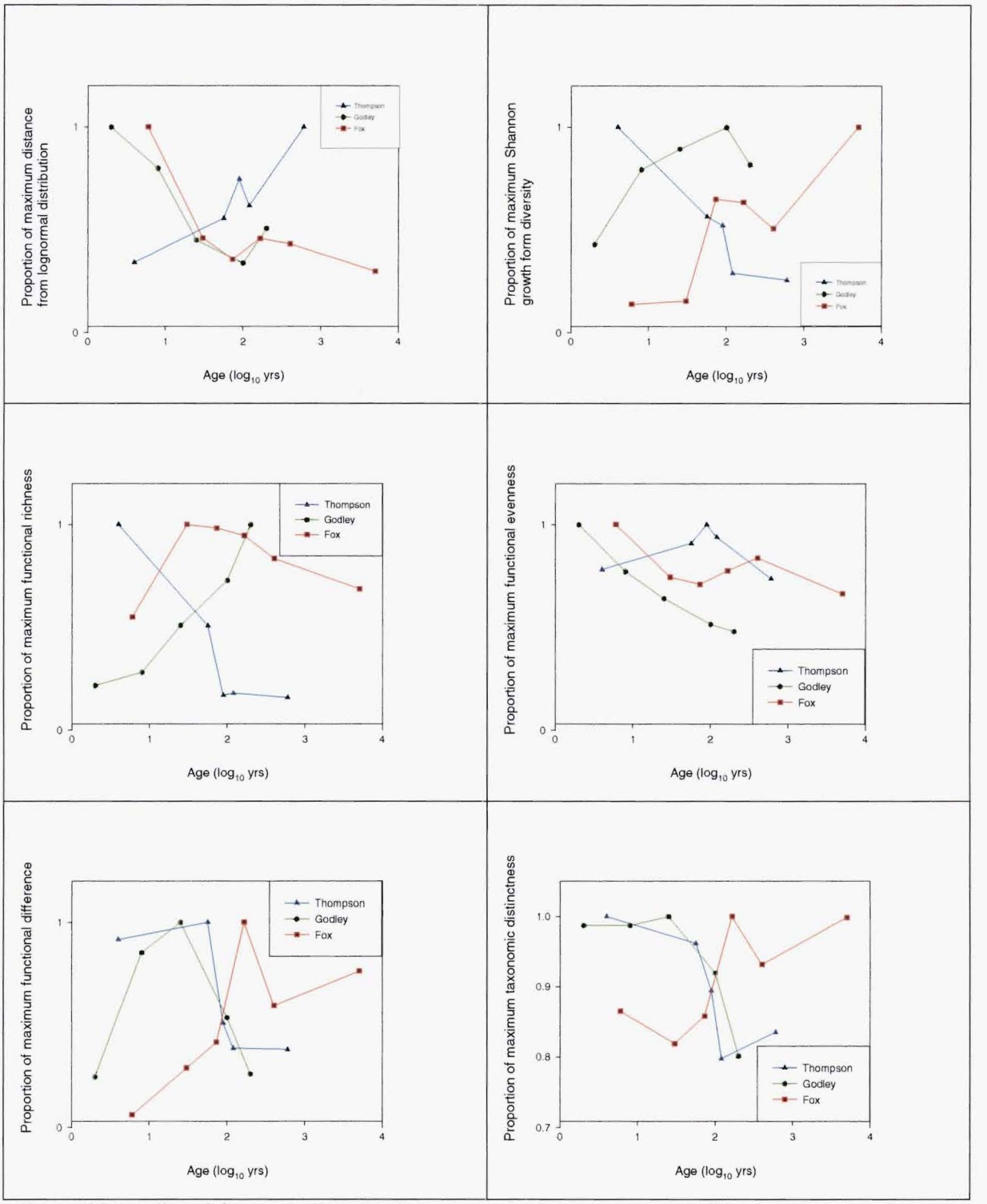


Figure 6.3 (continued from previous page) Normalised graphs to compare indices trajectories on the same y-axis scale in order to aid visual comparison of the trajectories. The mean values for each stage (same outlier samples removed as for regression analysis) of each site are normalised by converting them to a proportion of the maximum value for that site.

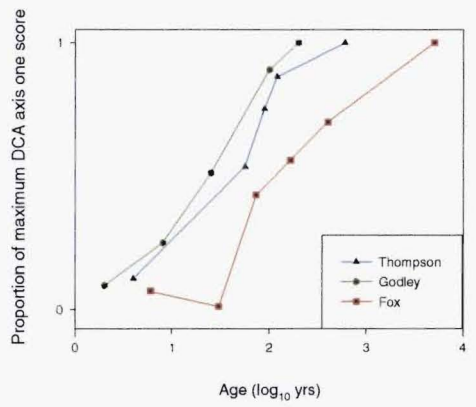


Figure 6.3 (continued from previous 2 pages) Normalised graphs to compare indices trajectories on the same y axis scale in order to aid visual comparison of the trajectories. The mean values for each stage (same outlier samples removed as for regression analysis) of each site are normalised by converting them to a proportion of the maximum value for that site.

6.4.2 SUMMARY OF INDEX RESPONSE PREDICTABILITY

Three categories of index response were identified in Figure 6.1. Two categories correspond to two levels of predictability, the third category is unpredictable. A summary of the index response behaviour that each category relates to as well as the results presented in sections 6.4.1.1 & 6.4.1.2 for index categorisation is given in Table 6.2. Only those indices in the two predictable categories qualify as useful for trajectory analysis.

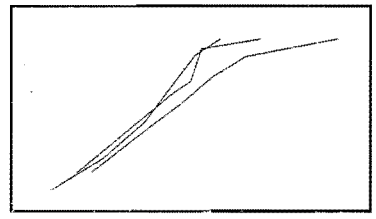
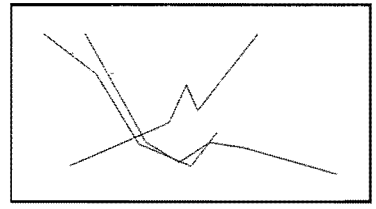
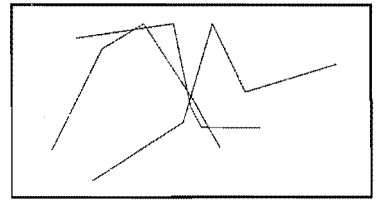
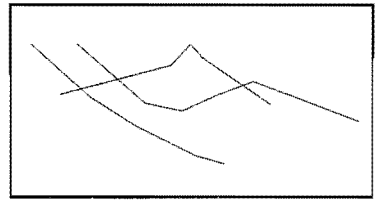
Index response category	Qualifying behaviour	Trajectory illustration	Index identities
Predictable with a universal trend direction	The index response was strong with a consistent trajectory and similar trend direction among study sites		pH Organic carbon Importance score DCA axis one
Predictable with different trend directions	The index response was strong with a consistent trajectory among all sites but trend direction was not similar among all sites		Simpson's diversity Distance from lognormal RAD Shannon's growth form diversity Taxonomic distinctness
Unpredictable	The index was sensitive to vegetation development among all sites but the trend was inconsistent in at least one site		Species density Functional richness Functional diversity
	The index was not sensitive enough to vegetation development in at least one site		Simpson's evenness Functional evenness

Table 6-2 An illustrated summary of the three categories of indexes in terms of their trajectory of response to the range of vegetation development gradients represented by the three study sites. The three categories correspond to the numbered outcomes of the flow chart depicted in Figure 6.1.

6.5 DISCUSSION

The aim of this discussion is to explain the ecological reasons behind why each index displayed the behaviour that led to its predictability classification according to Table 6.2. For detailed reasons why each index behaved as it did for each site see the discussion sections of Chapters three, four and five. In this chapter among site index behaviour is considered in the context of which ecosystem attribute the index primarily measures.

6.5.1 DEFINING ECOSYSTEM ATTRIBUTE TYPES

6.5.1.1 Function

The concept of ecosystem function is somewhat vague with different ecological authors describing function as the performance of different categories of processes including material and energy flow or the formation of biological structure and physical elements (Ehrenfeld 2000). However, function is generally perceived as the rate or dynamics of processes that cycle energy or nutrients through the system (Tilman 2001), such as primary productivity. Function as used in this thesis pertains to the rate or level of an ecosystem process[1].

Ecosystem maturity does not normally translate to the highest levels of energy cycling (i.e. function), rather the highest levels tend to be somewhere around the middle phase of succession with a decrease or levelling towards the end (Odum 1969). Nonetheless, the maintenance of a reasonably high rate of ecosystem process supports the persistence and resilience of an ecosystem (Palmer et al. 1997; Tilman et al. 1997), thus it is important to identify which indices track levels of function. Tracking levels of function is distinct from establishing that an ecosystem is functioning (i.e. some function occurring)

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[1] To avoid confusion, the definition of an ecosystem process used in this thesis is: 'Material or energy flow through or within an ecosystem as well as the formation of biological structure and physical elements'. See also definitions of other key thesis terms in section 1.6.

since a shift in the values of any ecosystem parameter can imply the latter, whereas the former requires the parameter to be specifically related to a process.

6.5.1.2 Structure

The concept of community structure, like that of function, does not have a clear and uniform definition throughout ecological literature (Samuels & Drake 1997). In the context of this thesis, structure is defined as any feature of the ecosystem components themselves (i.e. species) that does not deal with the identity of the species. Thus, structural parameters could include biomass, physiognomic strata, species or functional group relative abundances as well as alpha and beta species diversity (*sensu* Whittaker 1975). Crucially to this discussion, structure can be dependent on the species composition even though species are not identified, for example the RAD can be strongly influenced by the presence of a highly successful species that is able to dominate the assemblage.

6.5.2 WHICH INDICES ARE CORRELATED WITH ECOSYSTEM FUNCTION?

There is ample evidence to support the linkage of ecosystem function to both functional diversity (Chapin et al. 1997; Walker et al. 1999; Diaz & Cabido 2001; Tilman 2001) and also to the two traits used to calculate the four indices of functional diversity used in this thesis (Gates 1980; Aronson et al. 1993; Lavorel et al. 1997; Diaz & Cabido 2001). Taxonomic distinctness may also be correlated to function via its link to functional diversity (Petchey & Gaston 2002). However, it appears from the comparative results that neither the four functional diversity indices, nor taxonomic distinctness were highly correlated to function. The reasoning for this lack of correlation follows. As stated above, ecosystem function is expected to increase during succession, at least for the first part. The universal increase in importance scores would certainly indicate that this is the case for all the successions studied. For the same reason, if either the functional diversity indices or taxonomic distinctness were indeed highly correlated to function, one would expect to see increasing trends among sites, at least for the earlier part of succession. This was not the case.

There is much debate in the ecological literature about the relationship between plant species diversity and ecosystem process (e.g. Chapin et al. 1997; Tilman et al. 1997; Walker et al. 1999). As yet the issue remains unresolved but the consensus appears to be that although the two are linked, they are not directly related. There is evidence to suggest some level of functional redundancy within any species assemblage and this may be the

reason for the de-coupling (Loreau et al. 2002). Thus, species density and the two diversity indices related to proportional abundances of species (Simpson's diversity & evenness) are not expected to be closely linked to function. The results showing different trend directions among sites confirm this.

The only indices measured in this study that prior research suggests are highly correlated with ecosystem function, at least in young soils, are organic carbon and pH (Stevens & Walker 1970; Bormann & Sidle 1990). The results for these two indices showing common trends among two of the study sites support this correlation.

6.5.3 WHICH INDICES ARE CORRELATED WITH ECOSYSTEM STRUCTURE?

All indices tested in this thesis (other than soil properties) are based on structural aspects of the vegetation. Indices based on structural information may be relatively independent of composition, and could possibly be correlated with process (Walker & Langridge 2002).

6.5.3.1 What factors influence the predictability of structural indices?

It is postulated that the behaviour of a structural index depends on two factors: firstly, whether or not the index is linked to the process of succession and secondly, whether or not the index is dependent on assemblage composition.

6.5.3.1.1 Indices linked to succession but independent of composition

Those structural indices that have predictable trajectories with universal trends (importance score and DCA axis one) are thought to respond so because they are closely linked to successional gradients and are independent of composition. Indeed, importance score is a measure of biomass (Chiarucci et al. 1999) and the achievement of maximum biomass is a recognised as defining feature of plant succession (Odum 1969; Glenn-Lewin et al. 1992). Also, species turnover (the units of DCA axis one) is perhaps the most universal measure of succession (Miles 1987).

The similarity and asymptotic nature of the importance score trajectories indicates that all three study sites track primary succession from its inception until approximately its end-point, notwithstanding differences in rate and absolute values. This indication validates the comparisons made of all the indices among sites because although the

gradient lengths of vegetation development are different, the gradient length in terms of ecosystem development is the same.

6.5.3.1.2 Indices linked to succession but also dependent on composition

Structural indices that have predictable trajectories but which proceed in different directions among sites are: Simpson's diversity, Shannon's growth form diversity, distance from lognormal RAD and taxonomic distinctness. The consistent change exhibited by these indices suggests they are linked to successional gradients. The difference in trend direction among sites can be explained as a dependence on composition (which varies according to the environmental conditions and species pools prevailing at each site). Thus, whereas the successional process drives the structural change that these indices measure, this change is effected on different structural patterns among the assemblages, producing different gradients or trend directions. There are several studies mentioned in the discussion sections of Chapters three to five that demonstrate a strong linkage between succession and the structural parameters that this group of indices measure, although not always using identical indices to those in this study (Reiners et al. 1971; Grime 1979; Glenn-Lewin et al. 1992; Vetaas 1994; Bazzaz 1996; Kevan et al. 1997; Warwick & Clarke 1998a; Halloy & Whigham 2005). Yet none of these studies show a propensity for the trend direction to vary according to composition as occurred in this study with the Lake Thomson data set[2]. However, an extensive review of studies that have sought general responses to succession of community structural attributes similar to those measured by these indices, conducted by Samuels & Drake (1997), reported trajectory divergence to sometimes occur as a result of compositional differences.

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[2] It is likely that the Thomson site displayed different trends because of two factors. Firstly, many of the species in the species pool are able to colonise very early on, creating an early species density spike. Secondly, the habitat type that development tends towards is highly dominated by one species, in contrast to the other two study sites.

6.5.3.1.3 Indices that are dependent on composition but not linked to succession

Finally, unpredictable behaviour of structural indices can be explained by the index not being linked to succession whilst being dependent on composition. Thus, these indices effectively measure complex compositional gradients that do not respond in a uniform way to succession. The unpredictable group is comprised of all three functional diversity indices based on leaf area trait as well as Simpson's evenness and species density.

The unpredictability of the relationship between species density and succession is well documented (e.g. Whittaker 1977; Burrows 1990; Glenn-Lewin et al. 1992). The predictability of Simpson's diversity and distance from the lognormal RAD illustrates that aspects of the proportional abundances of species within assemblages do respond predictably to successional gradients. This suggests that Simpson's evenness measures an aspect of proportional abundance that does not respond predictably to successional gradients.

Functional richness, functional evenness and functional difference were untested measures for tracking long vegetation development gradients with leaf area data prior to this study. It would appear that the parameter of functional richness may respond predictably to successional gradients; the unpredictability stemming from the inadequacy of the index to measure the parameter. Thus, if the statistical properties of functional richness (specifically its sensitivity and variance) could be improved, it could be a promising index. On the other hand, the parameters that the functional evenness and functional difference indices measure do not appear to be suitable (at least with leaf area data) for tracking vegetation development.

6.5.4 FUTURE PERSPECTIVES ON ASSESSING TRAJECTORY SIMILARITY

For reasons stated in the methods and results sections, whilst ascertaining trajectory similarity is not a current priority for trajectory analysis, it may become so. The most promising field of research potentially able to provide suitable methods is pattern recognition. For example, two recent papers describe measures based on distance and similarity (Dickinson & Kraetzl 2004; Hidovic & Pelillo 2004).

6.6 CONCLUSION

On the basis of the definition of predictable and the associated comparative analyses presented in this chapter, a total of eight out of the original thirteen indices tested for their response to vegetation development are proposed to be suitable for restoration evaluation by trajectory analysis. The differences between the three case study systems (in terms of disturbance regime, environmental conditions, assemblage composition and structure as well as the time span of the successional gradients) indicate that these indices are suitable in a wide range of cases. The following final chapter discusses how the proposed indices could hypothetically be used for trajectory analysis. Ultimately, comparative testing of indices (such as is presented in this chapter), should be applied to multiple restoration case studies in order to test the validity of future trajectory estimates.

7 GENERAL DISCUSSION: USING PREDICTABLE INDICES OF PLANT COMMUNITY STRUCTURE FOR THE EVALUATION OF RESTORATION SUCCESS.

7.1 OVERVIEW

This thesis has investigated the response trajectories of various community indices to three vegetation development gradients inferred from the application of the chronosequence method to three distinct naturally recovering ecosystems. These indices summarise aspects of vegetation assemblage structure or soil development. Criteria applied to choose them over other available options were: relative ease of measurement and calculation as well as likelihood of sensitivity to disturbance recovery of vegetation. Chapters three to five described and explained the response behaviour of the entire range of indices tested to each of the three case study vegetation development gradients in turn. Chapter six compared the response of each index among the three case studies and classified the indices in terms of their level of sensitivity, consistency and trend similarity to all three development gradients. Only those indices classified in Chapter six as having predictable responses are considered to be potentially useful for restoration evaluation by trajectory analysis; therefore only these indices will be discussed in this chapter.

This chapter summarises the limited historical use of trajectory analysis to evaluate restoration and gives an opinion of its potential and a possible method of application to do so. Then, building upon interpretation in Chapter six regarding which community attribute (e.g. structure or function) the predictable sub-set of indices are most closely associated with, this chapter defines the restoration objectives and goals that each of these indices would be suitable to evaluate. In two further sections this chapter reviews past use of the predictable indices for restoration evaluation with any evaluation strategy and then gives a perspective on future possibilities for predicting ecosystem development trajectories. Finally, a hypothetical restoration project is outlined to provide an example of how the trajectory analysis strategy might be employed to evaluate success using multiple predictable indices. The primary focus of this chapters is to investigate the fourth and final thesis question.

Thesis question **IV**: *Which type of restoration goals are the indices suitable for trajectory analysis able to evaluate?*

7.2 INTRODUCTION

Before exploring thesis question four, a few issues of thesis scope covered in detail in the introduction must be re-addressed. The applicability of the conclusions about indices use for evaluation presented in this discussion is intended to be confined to restorations creating ecosystems with goals pertaining to either vascular plant assemblage characteristics or general aspects of ecosystem development. Some of the indices may be useful to evaluate restorations that begin with an existing ecosystem, i.e. that seek to deflect trajectories, rather than initiate them. Many would be appropriate for use with data from assemblages of other taxa. Nonetheless, these wider cases are beyond the scope of this discussion.

Trajectory analysis is focused on in this thesis for two reasons. Firstly, the use of trajectory analysis to evaluate restoration is at present relatively uncommon and in need of development (SER Science and Policy Working Group 2004). Secondly, it is postulated here that it is the most robust of the three evaluation strategies currently in use (i.e. direct comparison, attribute analysis and trajectory analysis; see section 1.3.2 for more detail) because it assesses the dynamics of the recovering system, rather than simply recording status at single point(s) in time. Thus, with regard to the conventional assumption that systems are capable of self sustaining change which is required to evaluate success for a still distant goal (e.g. Hobbs & Norton 1996), trajectory analysis would afford more confidence than confirming the same parameter value by direct comparison because of the additional evidence provided by the historic trajectory. A further advantage of trajectory analysis is that it is a simple and repeatable method. For this reason it should lead to a greater level of trajectory comparison among parameters and among restorations, thereby advancing restoration ecology as a science. Furthermore, frequent use of trajectory analysis should facilitate its own future development as a technique via the concomitant improved conceptualisation of ecosystem development and the effect of different restoration interventions.

In this chapter, the words index and parameter are used interchangeably; parameter refers to the ecosystem property that an index measures.

7.3 TRAJECTORY ANALYSIS

For restorations that seek to create ecosystems, success has to be evaluated on the basis of partial recovery. The trajectory analysis strategy of evaluating success is most suited to this scenario. This section gives a personal assessment of how the strategy would work and summarises the extent of its historic use.

7.3.1 THE TRAJECTORY ANALYSIS EVALUATION STRATEGY

Trajectory analysis is suitable to evaluate progress towards all goals that have a measurable parameter which is known to respond consistently to ecosystem or community development. Therefore, it can be used to evaluate success for a wide range of restoration endeavours. Trajectory analysis involves following the path of an ecosystem parameter constructed from periodic monitoring data of the recovering ecosystem. The time scale of monitoring required depends on the distance of the objectives; the minimum would be long enough for a consistent change to be established, whereas if the objectives were stringent the monitoring may have to continue until the trajectory pattern became evident. The evaluation of success involves making a judgement about whether the trajectory displays either similarity to a universal pattern or likelihood of approaching a reference target range. The type of pattern searched for depends on the type of goal and the parameter used to measure the goal. However, the confidence of evaluation judgements will reduce with increasing specificity of goal parameter values and distance from them at the time of evaluation because trajectories may not be entirely predictable even if future environmental conditions are assumed to be consistent with those at the time of evaluation.

A disadvantage of trajectory analysis is that, there is much empirical evidence to suggest that trajectory dynamics are only predictable to a certain extent[1] (Eiswerth &

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[1] It is recognised that the vegetation developments used to test index response consistency in this thesis are perhaps unrepresentative of the breadth of models describing community development because they all fit a deterministic model.

Haney 2001), owing to the probabilistic nature of community development (Pickett et al. 1987b; Drake 1990; Palmer et al. 1997) and threshold effects (Hobbs & Norton 2004) that are unforeseen. However, within current constraints of assembly rule understanding (Wilson et al. 1996) and lack of predictive modelling capability (Walker & del Moral 2003), assuming predictability is the only pragmatic solution (SER Science and Policy Working Group 2004) available to restoration ecologists. The need to evaluate restoration projects within human, rather than ecological, timescales in order to prioritise and reallocate scarce conservation resources (Holl & Howarth 2000; Hobbs & Harris 2001) and return mitigation bonds (Grant & Loneragan 2003) justifies evaluation judgements based on the assumption of predictability. Hopefully future restoration evaluations will be more certain of their predictions if encouraging developments being made in modelling trajectories (see section 7.6) become widely available.

7.3.2 HISTORIC USE OF TRAJECTORY ANALYSIS FOR EVALUATION OF RESTORATION SUCCESS

A review of papers published since 1990 was conducted using database searches to assess how commonly the trajectory analysis method has been used to evaluate restoration success (see Appendix one for a full list of citations).

The search was widened to include restoration in terrestrial and freshwater habitats, yet out of 35 projects only a few examples could be found of trajectory analysis use (i.e. where time series monitoring data was explicitly assessed for pattern) (e.g. Urbanska 1995; Simenstad & Thom 1996; vanAarde et al. 1996; Dawe et al. 2000; Brye et al. 2002; Asefa et al. 2003; Steyer et al. 2003; Wilkins et al. 2003; Penuela & Drew 2004). All of these studies except two (e.g. Simenstad & Thom 1996; Dawe et al. 2000) were not strictly applying trajectory analysis since monitoring was based at least in part on chronosequence data rather than direct continuous observation of the same site or sites. Also, even with the facility of the chronosequence method, the longest time span of recovery analysed was only 24 years. Furthermore, not all of these studies had specific reference information that provided a target, although all interpretations included implicit knowledge of the desired direction of change in the parameters measured. Moreover, none of these studies stated exactly what the goals were. Perhaps this explains why none of them stated whether success had been achieved, even though substantial positive progress had been made in many cases. Rather, they discussed whether or not improvements had occurred. In addition, the capacity of some of these studies to evaluate success using trajectory analysis

was limited by their use of unpredictable indices such as species richness (see Chapter six discussion section) (e.g. vanAarde et al. 1996; Asefa et al. 2003). Interestingly, the studies which did use indices that are likely to be predictable (e.g. parameters linked to ecosystem function, life form richness, cover abundance and PCA coordinates) and for which a consistent change was reported (Urbanska 1995; Simenstad & Thom 1996; Dawe et al. 2000; Steyer et al. 2003; Penuela & Drew 2004) made no specific use of their potential predictive power for evaluation of distant goals by extrapolation, except for Simenstad & Thom (1996). Instead, they evaluated whether or not the change that had occurred until the cessation of monitoring constituted an improvement, although Urbanska (1995) ventured to suggest that the observed vegetation development indicated the formation of a self-sustaining community. Perhaps for confident predictions to be made, there is still a prohibitive lack of long-term data sets describing the patterns, trends, and variability in parameter responses to perturbations, as well as natural variability in these parameters associated with dynamic equilibria.

With respect to the majority of the 35 reviewed papers that did not use trajectory analysis in any form, many authors simply did not have sufficient monitoring data of the correct type available to have the opportunity for employing the trajectory analysis strategy. However, some who did have sufficient data (i.e. time series data in a form that could be plotted on a two or three dimensional graph) referred to the concept of the recovery trajectory even though the evaluation was made without plotting a trajectory. For example, Parikh & Gale (1998) based the evaluation of increasing proximity to goals on progression of multivariate similarity as judged by cluster analysis, whereas de Souza & Batista (2004) established difference between each age using ANOVA statistics. Perhaps these authors felt evaluation by means of trajectories was insufficiently robust. Nonetheless, if statistical confirmation is required, trajectory analysis can be supported by the use of regression (e.g. Steyer et al. 2003).

7.4 EXAMINING THE UTILITY OF THE PREDICTABLE INDICES FOR TRAJECTORY ANALYSIS

As stated previously, all that is required of a 'useful' index is that it reliably exhibits consistent behaviour along gradients of vegetation development. At an individual project level, an index would be chosen to evaluate success on the basis of its ability to measure objectives that track progress towards a project goal. However, goals can be either specific or general, depending on whether they are based on reference system information or not. In recognition of the paucity of reference information it is suggested that an index able to assess a general goal (i.e. one which exhibits a universal response to community development) has a higher utility level. Thus, utility is synonymous with wide applicability.

7.4.1 IDENTIFYING OBJECTIVES AND GOALS RELATED TO EACH INDEX

A range of objectives that should be able to be evaluated collectively by all the predictable indices, as well as the goal to which each of these objective relates, are indicated in Figure 7.1. The objectives that each index is proposed to be able to evaluate and whether or not reference information is required in each case is summarised in Table 7.1. These goals and objectives have been devised by matching possibilities suggested by community ecology concepts with common restoration goals. For example, goal number two in Figure 7.1 is "persistent plant assemblage". This goal was derived for two reasons. Firstly, the end of primary succession has been linked to a dynamic equilibrium state with higher levels of community stability, self-organisation and persistence than when primary succession gradients are still active (Glenn-Lewin et al. 1992; Grimm & Wissel 1997; Palmer et al. 1997). Secondly, a persistent (or 'self-sustaining') community is a common restoration goal (SER Science and Policy Working Group 2004). Thus, objective '2b' in Figure 7.1 ("vegetation development is proceeding towards a dynamic equilibrium state") can be measured by importance score without reference information because importance score is strongly linked to the process of succession. Furthermore, a slowing of the rate of increase of importance score would suggest an approach to the final phase of primary succession in all systems. Figure 7.1 and Table 7.1 appear on the pages immediately following.

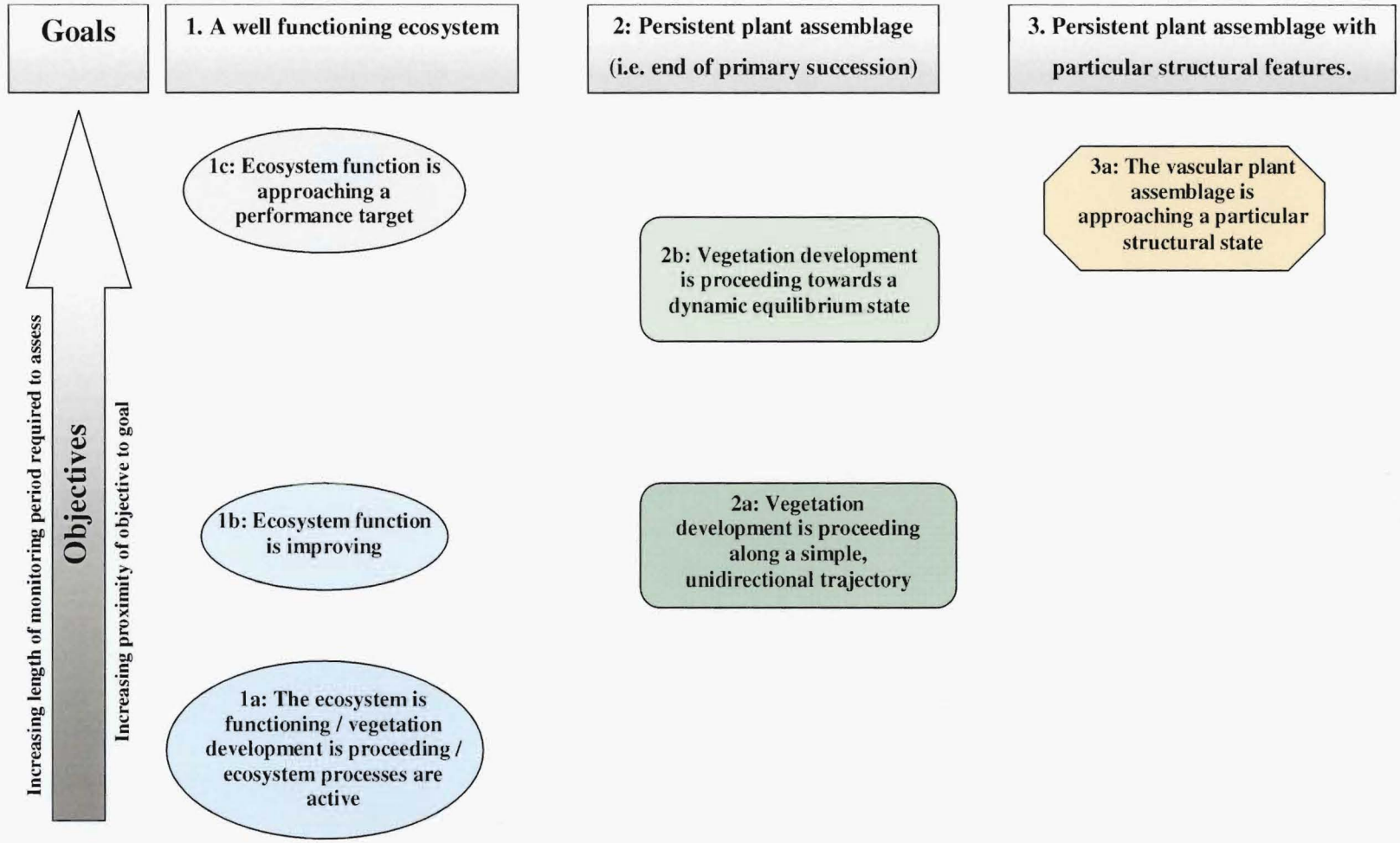

Figure 7.1 An illustration of the goals and objectives able to be evaluated using the predictable indices identified in this thesis. The goal which each objective relates to is identified by its number. Spatial proximity of the objectives to the goal equates to actual proximity and implies a longer monitoring period required to evaluate the objective.

Index	Response to vegetation development	Ecosystem attribute			Evaluation objective					
		Structure	Function	Process	1a	1b	1c	2a	2b	3a
Importance score	Predictable & universal	✓		✓	**✓**				**✓**	
DCA axis one	Predictable & universal	✓		✓	**✓**			**✓**	**✓**	
pH	Predictable & universal		✓	✓	**✓**	**✓**	✓			
Organic carbon	Predictable & universal		✓	✓	**✓**	**✓**	✓			
Simpson's diversity	Predictable	✓		✓	**✓**				✓	✓
Shannon's growth form diversity	Predictable	✓		✓	**✓**				✓	✓
Distance from lognormal distribution	Predictable	✓		✓	**✓**				✓	✓
Taxonomic distinctness	Predictable	✓		✓	**✓**				✓	✓

Table 7-1 Summary of the properties of each index in relation to their use for evaluation of restoration success. Information included for each index is; a) type of response to vegetation development, b) which ecosystem attribute they measure & c) which type of objective they are able to evaluate. Information classes a & b are summarised from Chapter 6. Evaluation objective numbers correspond with the goal definitions on the previous page (Figure 7.1). For goals 1&2, letters signify increasing proximity to goal with c being closest. Ticks in bold (objective section only) indicate that the objective can be evaluated without the need for reference information for the index concerned.

7.4.1.1 Interpreting trajectories: success or failure?

In practice, the actual trajectories that an evaluator would judge as signifying the accomplishment of an objective ('success') are envisaged to vary according to the index being used and whether or not reference information defines the objective in question.

On one hand, as illustrated in Figure 7.2a, if no reference information is required then success would be achieved if the indices' trajectories were confirmed to be following a consistent trend, regardless of the slope direction. For example, Table 7.1 shows this scenario would be the case for evaluating objectives '1a', '1b' and '2a' with all indices that relate to these objectives, and for objective '2b' with the two universal response indices only (importance score & DCA axis one). However, note that a decreasing trend cannot signify success for any objective for importance score, DCA axis one and organic carbon because no example is known of these decreasing in response to succession.

On the other hand, as illustrated in Figure 7.2b, if reference information is required then success would only be achieved if the indices not only had a trend with a consistent trajectory but also that the direction would be concordant with reaching the reference target. Table 7.1 shows this scenario would be the case for objectives '1c' & '3a' for all indices, and objective '2b' for those indices with non universal trajectories. Of course, Figure 7.2b does not illustrate a situation whereby trajectories plotted from monitoring data would have to decrease in order to approach the reference target; for example if objective '2b' was being evaluated with the distance from lognormal index. Nonetheless, for the case of an increasing trend being required, as is shown in Figure 7.2b, it is necessary to explain several key points of the graph. Firstly, the two green trajectories are considered indicative of success because, taking into account the x-axis scale discontinuity, they are the most likely trajectories to meet the reference target zone if they continue to change consistently. Such change could feasibly conform to a linear, asymptotic or sigmoidal trajectory. In contrast, the three red trajectories are indicative of failure because of inadequate response, inconsistent trajectory pattern or incorrect trajectory direction respectively. Secondly, the determination of failure for the inconsistent trajectory would probably not have occurred if the final value only had been taken, as would be the case if the direct comparison evaluation strategy had been employed. Thirdly, the graph clearly displays how difficult it is to be confident of successful accomplishment of distant objectives (as those set from reference states values by their nature are), even with predictable indices.

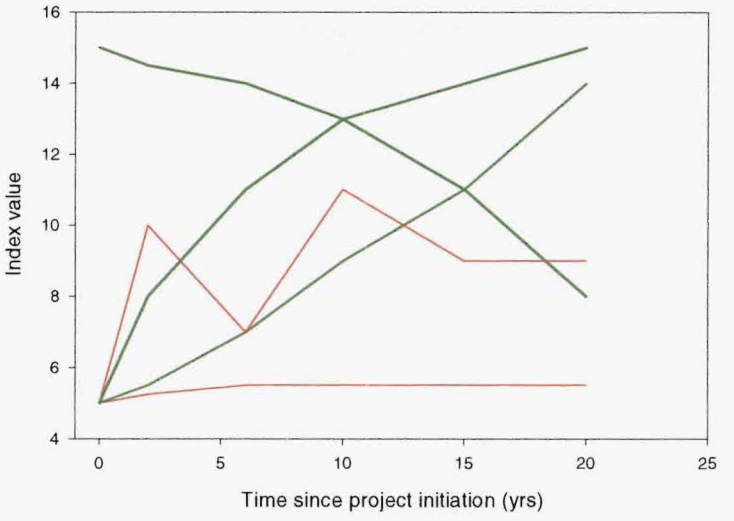

Figure 7.2 a Examples of the success and failure trajectories possible when objectives are not fixed value ranges set by reference information. Red lines are examples of trajectories that would lead to a judgement of failure to accomplish objective, green lines equate to success.

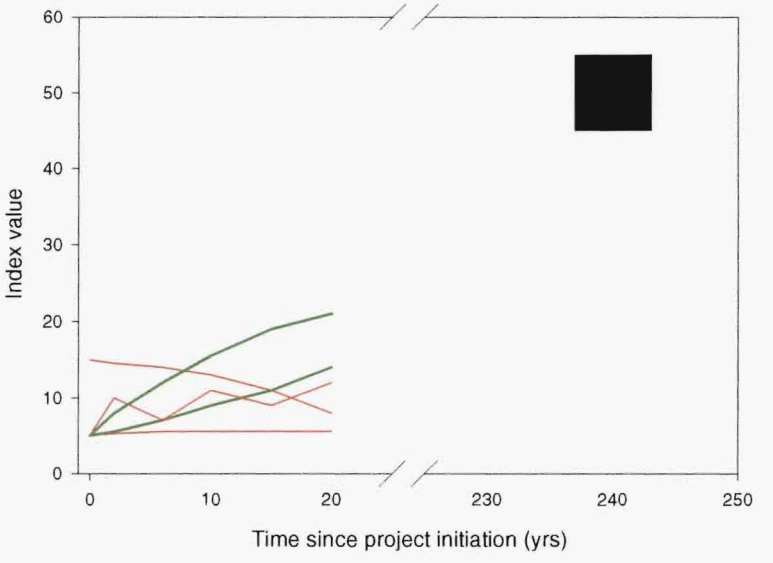

Figure 7.2 b Example of success and failure trajectories when reference information prescribes a target. Red lines are examples of trajectories that equate to probable failure of objective accomplishment, green lines equate to probable success. The solid square represents the objective; a target zone prescribed by the states of a number of reference samples with respect to the index parameter. N.B. the x-axis needs to be imagined without the discontinuity put in place to make the trajectories distinguishable on a realistic scale with respect to monitoring periods versus time for recovery to attain the objectives requiring reference data (1c, 2b & 3a).

Figure 7.2 Legend

Trajectory indicative of failure

Trajectory indicative of success

Reference target zone

As highlighted in the general introduction, making the assessment that accomplishment of objectives is likely to lead to achievement of goals requires the assumption that development will be self-sustaining (i.e. processes will continue without intervention). This assumption applies to all cases illustrated in Table 7.1. Furthermore, it is assumed that no perturbations will occur that might alter or arrest the trajectory (i.e. that if perturbations do occur then the system is resilient and therefore able to return to the same trajectory afterwards) and no unexpected thresholds will be reached.

7.4.2 HOW SHOULD THE PREDICTABLE INDICES BE APPLIED TO TRAJECTORY ANALYSIS?

An ideal scientific test of trajectory analysis effectiveness would be to study the response of a variety of indices to natural vegetation development as well as to various restoration interventions, within multiple ecosystem examples. The only feasible method to do this would be to use the chronosequence approach in both the naturally recovering ecosystems and those enhanced by restoration interventions. Unfortunately, within New Zealand (Atkinson 1994; Clout 1995; Meurk & Swaffield 2000; Saunders & Norton 2001) and worldwide (Dobson et al. 1997; Urbanska et al. 1997; Hobbs & Harris 2001; MacMahon & Holl 2001), restoration attempts do not have a long enough history and are not frequent enough within any one ecosystem to provide the level of replication necessary. Therefore, the method used in this thesis of studying the natural recovery aspect only and assuming that natural recovery represents a sufficiently close analogue to restoration recovery within the same ecosystem is the only available option, albeit a compromise.

7.4.2.1 Long recovery gradients are preferable

Ultimately, the predictable indices presented herein will need to be tested thoroughly by evaluating a variety of restorations in order to assess whether or not studying analogue natural recovery is a robust way to detect utility for restoration evaluation. In this way, variables which could affect the utility of particular indices would be identified. I propose that in the meantime a conservative definition of the type of restorations for which the indices presented in this chapter are most recommended for use is prudent. This definition parallels the characteristics of the analogue systems. For example, the length of potential vegetation development gradient until a dynamic equilibrium state is reached should be at least equivalent to the shortest gradient of the case

study systems. This caveat ensures sufficient developmental change is likely to have taken place within the probable time frame of evaluation in order to reasonably expect a strong enough response on which to base evaluation. Then, if no suitable response takes place (owing to thresholds for example) failure can be judged with some confidence.

7.4.2.2 Monitoring periods should be a few decades

A source of potential variation between the response trajectories in systems being restored versus naturally recovering systems is the sudden shift of some parameters induced by the acceleration of succession that intervention aims to achieve. However, this difference would normally be confined to the early stages and if the intervention were successful then autogenic processes should act to return the trajectory to a more normal course in time. To allow for this effect it is proposed that to facilitate effective evaluation monitoring must proceed for at least a couple of decades in order to discern that autogenic change has taken place.

7.4.2.3 Use of multiple indices per evaluation

The type of ecosystem attribute (e.g. composition/structure/function) that is most important to measure in order to evaluate restoration success is a matter of current debate in the restoration literature (e.g. Hobbs & Norton 1996; Ehrenfeld & Toth 1997; Palmer et al. 1997; Hobbs & Harris 2001; Choi 2004; Halle & Fattorini 2004; Mayer et al. 2004). This thesis makes no specific contribution to that debate because long term data sets tracking restoration recovery would be required to test which have most predictive power, and, the answer is likely to be system specific. Furthermore, although structure and function are intimately linked, relationships between the two are still not well understood (Simenstad & Thom 1996). Whilst conceptual guidance is lacking, it is perhaps best to take the approach of measuring at least one parameter of all three attributes. Certainly it would seem sensible to analyse the trajectory of more than one parameter to effectively evaluate success for several reasons. Firstly different parameters vary at different rates (Westman 1991). Secondly, interpretation of successional processes would be greatly facilitated, strengthening any evaluation judgements (see section 7.7 evaluation report example). The contribution of this thesis lies in suggesting some key parameters of structure and function that are useful to measure.

7.5 HISTORIC EVALUATION OF RESTORATION SUCCESS USING INDICES FOUND TO BE PREDICTABLE IN THIS STUDY

This section aims to further justify the use of the predictable indices for restoration evaluation and highlights where this research makes a novel contribution to the evaluators' 'tool-box'.

7.5.1 INDICES WITH PREDICTABLE TRAJECTORIES AND UNIVERSAL TRENDS

7.5.1.1 Importance score

Some measure of plant species cover abundance has been used commonly for the evaluation of restoration (e.g. Henry & Amoros 1996; Parikh & Gale 1998; Dawe et al. 2000; Vinther & Hald 2000; Prach & Pysek 2001; Seabloom & van der Valk 2003; Shuman & Ambrose 2003; Wilkins et al. 2003). Cover abundance has the flexibility to be measured for the whole assemblage or for parts of it, divided either by taxonomic (Parikh & Gale 1998), physiognomic (Wilkins et al. 2003) or growth form classifications (Asefa et al. 2003). The frequency with which cover abundance is applied to evaluation testifies to its utility, however, several of these authors report that plant abundance is able to reach levels of reference sites long before other facets of plant assemblage structure attributes have. This is a well documented effect during restoration (Westman 1991) and natural recovery (Odum 1969) and is a good example of the need to measure more than one parameter in order to effectively evaluate success.

7.5.1.2 DCA axis one

No examples using change in DCA axis one plotted against time (the 'DCA axis one' index referred to throughout this thesis) to evaluate restoration projects could be found. Whereas the use of ordination techniques to describe the composition of recovering plant assemblages is common. Some studies used ordination graphs to compare a single monitoring point with reference data (e.g. Bissels et al. 2004) simply to establish distance from the goal. Whilst more often ordination graphs were used to assess trends toward reference data (e.g. Reay & Norton 1999; Dawe et al. 2000; Paller et al. 2000; Wilkins et al. 2003), with some authors clarifying the trends by tracing illustrative trajectories. The advantage of using bi- or tri-axial ordination graphs (e.g. Figures 5.8 & 5.13 respectively)

is that progress towards and proximity to the target community type is very clear. However, the rate of change (species turnover) is not evident from these graphs, indeed no examples could be found of directly plotting any output of ordination against time for restoration evaluation. Furthermore, exact structural and compositional similarity of restored assemblages to reference ones is not a realistic goal. In contrast, plotting DCA axis one scores has the advantage that the consistency in direction of the main gradient of assemblage development is clearly illustrated as well as rates of species turnover being easy to interpret. A disadvantage is that there is no way to relate it to reference assemblages unless the length of successional gradients in the region are well known and invariable. Thus, in this context, plotting DCA axis one scores against time can be seen as a complementary alternative to conventional ordination graphs.

7.5.1.3 Soil chemical properties

The use of soil pH and organic carbon for evaluation is common (e.g. Bentham et al. 1992; Aronson et al. 1993; Vance & Entry 2000; Brye et al. 2002; Penuela & Drew 2004) but trajectory analysis of the monitoring data is relatively rare. It would be inadvisable to recommend their sole use, even if goals only relate to function, because rates of change vary along successional gradients and can be very slow. For example, Brye et al. (2002) found that both measures ceased to change after 19 years of prairie restoration despite a large discrepancy between observed and reference levels persisting. Nonetheless, their popularity is bound to endure because of ease of measurement, particularly for a parameter that relates so closely to ecosystem function.

7.5.2 INDICES WITH PREDICTABLE TRAJECTORIES

7.5.2.1 Simpson's species diversity

Species density is very commonly used to evaluate restoration projects (e.g. Parrotta et al. 1997; Newman & Redente 2001; Holl 2002). This is despite the fact that species density does not necessarily respond to ecosystem development in a consistent manner (Odum 1969; Glenn-Lewin et al. 1992) and so may not be an accurate index of recovery. Species diversity indices that take into account proportional abundances of species may be less volatile than species richness alone (Odum 1969) yet they are far less commonly measured (e.g. Grant & Loneragan 2003; Longcore 2003) and only one example (Asefa et al. 2003) could be found of their use in trajectory analysis.

7.5.2.2 Distance from the lognormal model of species relative abundance distribution

The sensitivity of the species RAD to assemblage change has been used in different ways for restoration evaluation. The tendency for assemblages of various taxa to approach lognormal has been used (e.g. Tacey & Glossop 1980), but has been more commonly applied to assessing degree of disturbance (e.g. Bell & Koch 1980; Kevan et al. 1997; Hill & Hamer 1998). An alternative method, where the change in RAD pattern is analysed by comparing the linear regression slopes of rank-abundance plots was recently suggested by Grant & Loneragan (2003) to be effective. Even though linear regression looses information, this is a vast improvement over traditional methods of RAD analysis that have involved either fitting curves by eye (e.g. Tacey & Glossop 1980), or lengthy comparisons of deviance from multiple models (Wilson 1991). However, the distance from lognormal measure presented in this thesis goes one step further since it gives a comparable value for each monitoring point that is easy to interpret and enables trajectory analysis. Furthermore, this measure provides a convenient quantification in shift of RAD pattern whose utility transcends that of the mechanism used to derive it; i.e. fitting data to a specific RAD model.

7.5.2.3 Shannon growth form diversity

No examples of a growth form diversity measure (one incorporating growth form richness and relative abundance) being used as a restoration evaluator could be found. Whereas growth form richness is a relatively commonly used evaluation measure (e.g. Urbanska 1995; Asefa et al. 2003). However, Seabloom (2003) experimented with another type of growth form diversity which analysed shifts in species richness within growth form categories. It is proposed here that the use of proportional growth form abundances is a natural extension to the use of growth form richness alone, since it encapsulates the evenness component of diversity. Furthermore, it would seem logical that as growth form diversity includes more information it would be more sensitive to assemblage change than richness alone, especially since the number of growth forms tends to be low.

7.5.2.4 Taxonomic distinctness

Despite the different information provided by the inclusion of taxonomic relatedness into species diversity indices (Pielou 1975; Magurran 2003), no examples could be found of the use of such indices to asses restoration success[1]. Research has shown the latest of such indices, the taxonomic distinctness (Warwick & Clarke 1995) index used in this thesis, to be sensitive to disturbance and successional gradients (Warwick & Clarke 1995, 1998a) of marine animal assemblages. In addition, this research has shown it to respond predictably to plant assemblage succession. On these bases, it would appear to be a very promising evaluation measure. Furthermore, because the taxonomic information included links the index more closely to functional diversity than to species diversity (Diaz & Cabido 2001; Magurran 2003), it provides an opportunity for improving evaluators ability to make much sought inferences about ecosystem function.

7.6 FUTURE PERSPECTIVES ON PREDICTING RESTORATION SUCCESS

7.6.1 A SYNERGY BETWEEN THE HOLISTIC AND REDUCTIONISTIC APPROACHES TO CONCEPTUALISING ECOSYSTEM DEVELOPMENT?

The central premise of trajectory analysis is that future ecosystem development is to some extent predictable on the basis of observed historic pattern. Whilst this is reasonable, the reality is that ecologists have been unable to predict the development of any assemblage with certainty (Walker & del Moral 2003). Therefore, in order for the

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[1] This statement may cause some confusion since 'Taxonomic diversity' is sometimes cited as an evaluation measure in the restoration literature (e.g. Paller et al. 2000). However, close examination of the methods reveals that authors are referring to richness within higher hierarchical taxonomic levels (e.g. number of families) or number of species within a taxonomic guild, rather than the index devised by Warwick and Clarke (1995).

accuracy of predictions to increase, better understanding of ecosystem development and behaviour is required. There are two broad research approaches toward increasing the ability to predict that can be traced back to the two different perspectives evident in the early development of ecological succession theory. Firstly, there is the holistic approach rooted in Clements' (1916) ideas that system behaviour cannot be explained simply by studying its components; the 'organismal' analogy. A modern manifestation of this view is the field of complex systems theory that focuses on whole system emergent properties rather than the component species. Secondly, there is the reductionism approach that Gleason (1917) is credited to be the progenitor of with his idea that system behaviour can be entirely explained by understanding the interactions of the component species. Recent developments of the reductionism approach include modelling multiple factors to predict the outcome of the assembly process. Developments of these two apparently distinct approaches that could apply to restoration evaluation are summarised in the following paragraphs. In my view, it is likely that the two approaches will work synergistically to achieve a better resolution of what factors affect the recovery trajectory predictability, as has occurred over the past century with successional theory. Nonetheless, it will be a long time before restoration ecologists will pass the test of understanding set by Jordan et al. (1987) whereby they will be able to reliably reconstruct or create resilient communities with specific structural and functional dimensions. Hopefully the twin motivations of scientific curiosity and the accelerating societal need for effective rehabilitation of ecosystems (Young et al. 2001) will provide the inertia to solve the issues.

7.6.2 THE REDUCTIONISTIC APPROACH: INDIVIDUALISTIC MODELS

There has been some success with prediction of assemblage structure and composition of assemblages being restored based on successional models that take into account life history characteristics of the species present (e.g. Roberts 1996; Twilley et al. 1998). However, these models require high volumes of ecological data particular to the species concerned and because their assumptions are based on relatively simple systems (Wilson et al. 1996) cannot hope to encompass the possibilities of multiple trajectories and alternative stable states (Walker & del Moral 2003). Furthermore, at present the models are not able to link processes such as species turnover, nutrient turnover and biomass accumulation and tend to be decoupled from ecosystem function (Thompson et al. 2001). Future models must take into account establishment and extinction probabilities under changing environmental conditions (Petchey et al. 1999), priority effects of establishment

order (Walker & del Moral 2003) as well as the effects of perturbations at different stages in development (Chapin et al. 1997; White & Jentsch 2001). In order to support the increasing complexity of models, the development of analytical tools based on non-linear mathematics needs to continue until they are able to adequately describe the non-linear dynamics of ecological processes, threshold effects, species interactions and species environment relationships (Thompson et al. 2001).

7.6.3 THE HOLISTIC APPROACH

7.6.3.1 Resilience and convergence models

Simpler ways of modelling trajectories have also been suggested. For example, Westman (1991) noted that two components of resilience could be used; 'elasticity' (rate of recovery) and 'damping' (the extent of trajectory oscillation). To use elasticity, multiple examples of natural recovery in the same system as is being restored must have been previously studied so that early rates of restoration recovery can be used to predict future rates by matching response curves with the reference data. The damping of a parameter, such as change of assemblage in ordination space, can be assessed by calculating the ratio of oscillations to the length of the straight line trajectory. High ratios indicate that other parameters will have predictable trajectories. Wassenaar & Ferreira (2002) proposed a method for developing convergence models to test the likelihood of and time frame for an ecosystem returning to its pre-disturbance state based on the performance displayed by monitoring data. However, the model's accuracy relies on either data being available from previous successions in similar habitats, or enough examples to construct global rules.

7.6.3.2 Complex systems theory: identifying emergent properties of self-organised systems

Complex systems theory has its roots in cybernetics (Patten & Odum 1981); the study of connection between components of any system focusing particularly on feedback loops that was responsible for the evolution of the digital computer. Modern complex systems theory has successfully been applied to many fields of the biosciences throughout the 1990s including theoretical ecology (Sole & Levin 2002), yet its principles have not been taken up by restoration ecology. Excellent descriptions of how the theories relate to the dynamics of ecosystems (Kauffman 1993; Depew & Weber 1995; Patten & Jørgensen 1995; Bak 1996; Jorgensen et al. 1998; Drake et al. 2001b) and vegetation assemblages

(Anand 2000) exist, therefore a brief précis of the aspects of complex systems theory relevant to prediction of ecosystem dynamics is given here.

Provided that disturbances are not too frequent or intense, the continuous uptake and transfer of energy through ecosystems means that through species interactions and feedback loops, the system becomes 'self-organising'(Bak 1996). Self-organisation in turn creates emergent system properties such as structural regularities (Halloy & Whigham 2005), patterns of functional performance (Jorgensen et al. 1998) and structural trajectory shape (Anand & Desrochers 2004). Despite growing theoretical effort, the relationship between self organisation and mechanisms of succession are unknown (Weiher & Keddy 2001). However, a key point of the theory for trajectory analysis is that 'attractors' of different types define possible states and trajectory dynamics (Anand & Desrochers 2004). Thus, the theory invokes higher order processes than successional mechanisms to explain how ecosystem dynamics and structure evolve.

There are two ways that complex systems theory could be applied to the evaluation of restoration using methods in existence. Firstly, information indices (e.g. Margalef 1968; Aoki 1993) (which have also been incorporated into the concept of ecosystem health (Mageau et al. 1998)) supposedly measure a higher level order within developing ecosystems that is a more predictable, if less specific, parameter than any based on structure or function. These indices measure the efficiency of energy transfer within the system which is thought to increase steadily as any system recovers from a perturbation (Odum 1985; Patten & Jørgensen 1995); i.e. as the system becomes increasingly self-organised. Thus, a steady increase in an information index during restoration recovery monitoring would provide a very robust indicator of the system being self-sustaining. The second application of complex systems theory would be the visual or statistical analysis of structural trajectories to assess what type of 'attractor' the system is responding to. Anand & Desrochers (2004) illustrate the type of trajectory pattern different attractors might create and assess how this can predict the consistency of future trajectories of several successional data sets. They do not cite any examples of the technique's use for restoration evaluation, nevertheless, it could serve as a good general tool provided monitoring periods are sufficiently long to establish dynamics.

7.7 TRAJECTORY ANALYSIS EVALUATION EXAMPLE

The hypothetical example of a restoration project described here is an example of the more specific of the two types of restoration identified in the general introduction as being able to be evaluated by the methods suggested in this thesis; i.e. 'Creation of a new ecosystem of the same kind to replace one that has been entirely removed'. The aim of including this example is to clarify the way in which an evaluation might be conducted using some of the indices proposed in this thesis as useful for trajectory analysis methods.

7.7.1 PROJECT BRIEF

An exhausted mine site devoid of soil and vegetation is to be restored to native forest vegetation. The company responsible for mining must undertake restorative actions so that it can provide reasonable evidence within 35 years of starting restoration that the site will continue towards the goals. If the restoration is successful, the company would stand to receive a mitigation bond back from the government and could expect future consent applications to be assessed more favourably.

The mine site is surrounded by native vegetation. The region is subject to an active natural disturbance regime of wind-throw and landslides, creating a patchwork of different vegetation states and introducing considerable structural variation into any given state. Nonetheless, there is sufficient ecological knowledge of the system to define the range of states from which to collect baseline reference information. The nature of the disturbance regime means that a chronosequence of natural primary succession can not be found in order to construct a model of typical vegetation development. Thus, reference information is confined to a description of the plant assemblage that appears to be the most stable state attained. Restoration attempts have been made in the region before but they have not been adequately monitored enough to provide an expectation of how recovery will progress. Therefore, evaluation will be used not only to assess success but also to adapt the restoration interventions. Planned interventions are replacement of topsoil and planting of woody successional species.

7.7.2 EVALUATION PLANNING

The vision, goals and objectives have been defined as follows:

- **Vision**

  Fully functioning indigenous forest ecosystem of similar community structure and composition to reference sites.

- **Goals**

  1. Well functioning ecosystem (=goal # 1 of Figure 7.1).
  2. Persistent plant assemblage (=goal # 2 of Figure 7.1).
  3. Persistent assemblage with structural features like those of the reference site (=goal # 3 of Figure 7.1).
  4. Compositional similarity to reference site.

- **Short term objectives; to be evaluated at five years**

  1a. The ecosystem is functioning / vegetation development is proceeding / ecosystem processes are active (=objective #1a of Figure 7.1).

  1b. Ecosystem function is improving (=objective # 1b of Figure 7.1).

- **Medium term objectives; to be evaluated at 35 years**

  2a. Successional trajectory is directional (=objective # 2a of Figure 7.1) .

  3a. The vascular plant assemblage is approaching a particular structural state (=objective # 3a of Figure 7.1).

  4a. assemblage includes key plant species (canopy dominants) and faunal species (dispersers).

Note that all goals and objectives are those presented in Figure 7.1, except for goal four and objective '4a'. Objective numbers signify which goal they relate to. All objectives are able to be evaluated solely by indices tested in this thesis except for objective '4a' which requires species identity information. The species composition information of objective 4a is included because although this thesis has focused on indices of community structure so as to have generic applicability, it is recognised that any restoration evaluation is bound to include compositional objectives of some kind. In addition, the presence of keystone species such as those in objective '4a' are likely to influence structural state.

7.7.3 MONITORING PROTOCOL

10 by 10 metre vegetation plots are established in the first year after plantings. Sufficient numbers of plots are established so as to encompass the variation that exists within the restoration site. However, plot numbers are limited so they will not be disproportionate to the restoration area or lead to excessive amounts of effort. In all plots cover abundance is measured for all vascular plant species and soil samples are taken. Basic abundance data for key avian dispersers of plant propagules is recorded whilst in plots measuring plants. Monitoring measurements are made every year for the first five years and every five years thereafter until the 35 year project term is completed.

Vascular plant data are used to derive values for four indices; Importance score, DCA axis one, Simpson's diversity and distance from the lognormal distribution. To aid interpretation of the two indices based on relative abundances of species, rank-abundance plots are drawn. In addition, the abundance of key canopy bird species is plotted. Soil samples are used to measure amounts of organic carbon.

7.7.4 EXAMPLE OF THE EVALUATION SUMMARY

After five years the importance score has steadily risen, as has the concentration of organic carbon. Therefore success has been achieved for both the short term objectives ('1a' & '1b').

After thirty five years, importance score and Simpson's diversity show trajectories that are moving towards the reference state (both being higher values). However, Simpson's diversity has not moved very far. Also, distance from lognormal is not showing any definite trajectory. The rank-abundance graphs indicate that although species density has risen, the restoration plantings remain dominated by the planted species which consisted of only a few species. Therefore, the abundance of other species is low. This explains why Simpson's diversity has not increased very much. It also explains why distance form lognormal shows no trend; because the assemblage structure has not made much progress towards a mature assemblage. However, DCA axis one shows that there was a definite successional process taking place and that the assemblage appears to have developed in a progressive direction, albeit with a limited gradient. Therefore, there must have been some consistency in the species additions that rank-abundance plots showed to have occurred on the restoration site, both over the time span and among replicate samples. In particular, some individuals of key canopy species became established during the final

monitoring period; this suggests that the directional successional process identified by the DCA axis one index will tend towards the reference community composition and structure in time. The presence of key avian dispersal agents, although not abundant, also supports the conclusion that succession will tend towards the reference composition since they should ensure that all the species of the reference community will be able to arrive in the restoration site. The levels of organic carbon continued to rise, suggesting that the soil would be able to support continued vegetation development.

In conclusion, despite quite slow progress it is possible to judge that success has been achieved for objectives '2a', '3a' & '4a'. This judgement was only possible by virtue of the complementary information that the different components of monitoring information gave. Moreover, confidence that the monitoring values are part of an ongoing pattern, made possible using the trajectory analysis method, would have been essential to have made these judgements in the time period concerned and with the hypothetical responses described.

7.8 SUGGESTIONS FOR FURTHER RESEARCH WORK

Naturally, at least as many questions were raised by this thesis than were answered by it. I would suggest the following priorities for further research toward improving our ability to evaluate the success of restoration interventions:

- Studies of succession in more seres and also among duplicates of seres to test the generality of successional theories.
- More consistency in methods of evaluation of restoration sites. This would enable the comparison of index recovery patterns both within and among ecosystems and over different time scales.
- Interdisciplinary studies in a range of ecosystems examining variation of parameters at different levels of organisation (population/community/ecosystem/ landscape) as well as temporal/spatial scales. Results should be examined with a view to developing community ecology theory regarding linkage of structure, function and process.
- Studies to compare the spatial and temporal patterns during primary succession of plant assemblage structure with that of various other taxa, especially those closely linked to function (e.g. microbes and insects).

- Development of complex systems theories to establish measurable universal indicators of self-sustaining systems based on the emergent properties of a self-organised state.
- More work on establishing assembly rules and using them to build individualistic models to improve the predictability of successions.
- Studies of the effects of plant-plant as well as animal-plant interactions on successional trajectories and rates especially alien herbivores on native plants.
- Long-term ecosystem monitoring including controlled perturbations focused on ascertaining measurable properties that create or indicate resilience.

7.9 CONCLUSION

This chapter provides a framework within which the predictable indices obtained from this research could be used for restoration evaluation by trajectory analysis. Furthermore, it emphasises how the use of these indices with trajectory analysis (alone or in combination) represents a promising strategy for evaluating some types of restoration projects. Nonetheless, extensive testing is required to establish how widely applicable these indices are, in particular with respect to monitoring periods required and confidence limits of success judgements.

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APPENDIX ONE: REFERENCES COMPRISING THE LITERATURE SEARCH ON RESTORATION EVALUATION PARAMETER USE FREQUENCY

A summary table (Table 1.1) of the indicators used to evaluate restoration success that were reported in 35 peer reviewed English language journal papers published from 1990 to 2004 was given in Chapter one (page 9). The citation list is given here: (Bentham et al. 1992; Nelson 1993; Duel et al. 1995; Urbanska 1995; Weller 1995; Henry & Amoros 1996; Simenstad & Thom 1996; vanAarde et al. 1996; Andersen & Sparling 1997; Mayer & Galatowitsch 1999; Reay & Norton 1999; Curnutt et al. 2000; Jorgensen et al. 2000; Paller et al. 2000; Short et al. 2000; Block et al. 2001; Bailey & Covington 2002; Brooks et al. 2002; Brye et al. 2002; Findlay et al. 2002; Hylander et al. 2002; McCoy & Mushinsky 2002; Pereira et al. 2002; Asefa et al. 2003; Grant & Loneragan 2003; Longcore 2003; Parkyn et al. 2003; Seabloom & van der Valk 2003; Steyer et al. 2003; Wilkins et al. 2003; Abella & Covington 2004; Bissels et al. 2004; Harden et al. 2004; Nassauer 2004; Penuela & Drew 2004).

APPENDIX TWO: NEW ZEALAND MAP GRID SAMPLE PLOT COORDINATES FOR ALL SITES

Given below are map coordinates for each of the plots sampled during the course of this study. All coordinates have been calculated using the New Zealand Map Grid (1949) projection. Coordinates were attained using a hand-held GPS device with the following accuracy.

Site:	**Range of accuracy for the coordinates:**
Thompson	6 to 12 m
Fox	7 to 14 m
Godley	3 to 6 m

Note: At the Fox and Thomson sites the blanks are incidences where accurate coordinates were not able to be attained for sample plots using the hand held GPS device due to dense forest canopy cover or topography.

COORDINATES FOR THE THOMSON SITE

Sample Plot ID	Development Stage	Easting	Northing
0a	1	2079562	5559928
0b	1		
0c	1		
0d	1	2079542	5559907
0e	1		
0f	1		
0g	1	2079464	5559856
0h	1	2079432	5559837
0i	1	2079402	5559808
0j	1		
1a	2		
1b	2	2079550	5559882
1c	2	2079546	5559879
1d	2	2079524	5559865
1e	2		
1f	2		
1g	2	2079554	5559869
1h	2		
1i	2		

1j	2		
2ar	3		
2b	3	2079615	5559840
2c	3		
2d	3	2079568	5559796
2f	3		
2g	3		
2h	3	2079601	5559812
2i	3	2079564	5559812
2j	3		
3ar	4		
3b	4	2079579	5559846
3c	4	2079550	5559827
3d	4	2079536	5559816
3e	4		
3f	4		
3g	4		
3h	4		
3i	4		
3j	4	2079523	5559830
4ar	5		
4b	5	2079679	5559730
4c	5	2079678	5559726
4d	5	2079674	5559680
4e	5	2079678	5559789
4f	5		
4g	5		
4h	5		
4i	5		
4j	5		

COORDINATES FOR THE GODLEY SITE

Sample plot ID	Development Stage	Easting	Northing
GO014	1	2306543	5737972
GO026	1	2307719	5736946
GO042	1	2306899	5736972
GO045	1	2307206	5736413
GO063	1	2306423	5737731
GO068	1	2306419	5735952
GO071	1	2306555	5735248
GO072	1	2306715	5735016
GO073	1	2306777	5735024
GO075	1	2306568	5735351
GO076	1	2306608	5736237
GO077	1	2306606	5736213
GO078	1	2306592	5736107

GO083	1	2306693	5735967
GO084	1	2306779	5736052
GO113	1	2306926	5735256
GO114	1	2306983	5735376
GO115	1	2307075	5735340
GO116	1	2307055	5735235
GO118	1	2307337	5735277
GO119	1	2307280	5735819
GO139	1	2306715	5737890
GO140	1	2306824	5737593
GO141	1	2306929	5736777
GO142	1	2306959	5736654
GO143	1	2306975	5735826
GO143-	1	2306955	5735972
GO144	1	2306761	5735448
GO145	1	2306731	5735159
GO151	1	2308183	5735408
GO152	1	2308249	5735717
GO165	1	2307719	5736529
GO166	1	2307239	5736564
GO015	2	2306680	5737924
GO016	2	2306855	5737971
GO020	2	2307690	5737656
GO022	2	2307730	5736393
GO024	2	2307774	5737083
GO025	2	2307756	5736992
GO031	2	2307537	5737443
GO032	2	2307342	5737504
GO039	2	2307078	5737313
GO040	2	2307033	5737425
GO041	2	2306928	5737326
GO043	2	2307250	5736948
GO044	2	2307135	5736490
GO048	2	2307084	5736357
GO049	2	2307002	5736491
GO053	2	2307629	5736078
GO059	2	2308206	5735892
GO061	2	2308066	5736009
GO064	2	2306517	5737313
GO065	2	2306544	5736860
GO066	2	2306589	5736770
GO074	2	2306689	5735360
GO079	2	2306567	5736036
GO080	2	2306356	5735289
GO081	2	2306442	5735483
GO082	2	2306492	5735843
GO085	2	2307020	5735965
GO086	2	2306987	5735772

GO117	2	2307119	5735228
GO017	3	2307284	5737987
GO018	3	2307902	5737828
GO019	3	2307785	5737932
GO021	3	2307806	5736446
GO023	3	2307727	5736213
GO027	3	2307900	5736744
GO028	3	2308070	5736364
GO029	3	2308122	5736276
GO033	3	2307269	5737564
GO034	3	2307325	5737689
GO035	3	2307406	5737770
GO036	3	2307397	5737914
GO037	3	2307341	5737990
GO038	3	2307172	5737877
GO046	3	2307279	5736318
GO047	3	2307151	5736146
GO050	3	2307296	5736055
GO051	3	2307361	5736076
GO052	3	2307516	5736005
GO054	3	2307839	5736171
GO067	3	2306521	5736319
GO069	3	2306295	5735593
GO070	3	2306348	5735031
GO111	3	2306309	5735687
GO112	3	2306421	5735334
GO129	3	2308183	5736460
GO146	3	2307992	5735024
GO147	3	2308068	5735147
GO148	3	2308114	5735159
GO149	3	2308065	5735179
GO150	3	2307800	5735100
GO056	4	2308066	5736375
GO087	4	2308246	5735844
GO090	4	2308006	5736541
GO091	4	2308167	5736449
GO093	4	2308219	5735903
GO095	4	2308294	5735748
GO096	4	2308324	5735654
GO097	4	2308268	5735690
GO098	4	2308176	5735485
GO099	4	2308254	5735222
GO100	4	2308272	5735187
GO101	4	2308299	5735169
GO104	4	2308182	5735555
GO106	4	2308258	5735630
GO107	4	2308274	5735692
GO108	4	2308239	5735812

GO110	4	2308072	5736340
GO121	4	2308142	5736485
GO124	4	2308156	5736462
GO128	4	2308171	5736432
GO132	4	2308139	5736468
GO134	4	2308188	5736340
GO136	4	2308247	5736324
GO154	4	2308232	5736362
GO155	4	2308214	5736395
GO156	4	2308253	5736401
GO157	4	2308272	5736382
GO160	4	2308101	5736556
GO163	4	2308044	5736602
GO164	4	2308119	5736515
GO030	5	2308291	5736430
GO055	5	2308177	5736231
GO057	5	2308216	5736342
GO058	5	2308132	5736532
GO060	5	2308310	5735838
GO088	5	2307963	5736623
GO089	5	2307965	5736614
GO092	5	2308218	5736380
GO094	5	2308258	5735853
GO102	5	2308326	5735121
GO103	5	2308162	5735563
GO105	5	2308186	5735545
GO109	5	2308232	5735962
GO120	5	2308151	5736514
GO122	5	2308218	5736520
GO123	5	2308201	5736516
GO125	5	2308156	5736534
GO126	5	2308139	5736510
GO127	5	2308177	5736487
GO130	5	2308186	5736444
GO131	5	2308234	5736502
GO133	5	2308177	5736414
GO135	5	2308211	5736339
GO137	5	2308184	5736410
GO138	5	2308185	5736383
GO153	5	2308191	5736386
GO158	5	2308225	5736332
GO159	5	2308091	5736587
GO161	5	2308120	5736566
GO162	5	2308084	5736603

COORDINATES FOR THE FOX SITE

Sample plot ID	Development Stage	Easting	Northing
J1	1	2271780	5741081
J2	1	2271812	5741073
J3	1	0	0
J4	1	0	0
J5	1	2271796	5741160
J6	1	0	0
I1	2	2269977	5741934
I2	2	2270005	5741963
I3	2	2270029	5741970
I4	2	2227020	5741991
I5	2	0	0
I6	2	2269966	5741974
I7	2	0	0
I8	2	0	0
I9	2	2269948	5741969
G1	3	2269979	5742235
G2	3	0	0
G3	3	2270006	5742177
G4	3	2270010	5742072
G5	3	0	0
G6	3	0	0
G7	3	2270246	5741870
G8	3	2272072	5742066
G9	3	0	0
E1	4	0	0
E2	4	2269777	5742232
E3	4	2269780	5742193
E4	4	0	0
E5	4	2269798	5742108
E6	4	0	0
E7	4	2269762	5742284
E8	4	0	0
E9	4		
B1	5	2269406	5742333
B2	5	2269368	5742458
B3	5	0	0
B4	5	2269331	5742534
B5	5	0	0
B6	5	0	0
B7	5	2269360	5742577
B8	5	0	0
B9	5	2269278	5742536
A1	6	2268687	5743560
A2	6	0	0

A3	6	0	0
A4	6	2269000	5743600
A5	6	0	0
A6	6	0	0
A7	6	0	0
A8	6	0	0
A9	6	0	0

APPENDIX THREE: GROWTH FORM CATEGORIES

Growth form category descriptions modified from Druce (1993). Categories are defined from a mixture of growth form and phylogenetic information.

Growth form category #	Growth form category description
1	Gymnosperm trees & shrubs
2	Monocotyledonous trees & shrubs
3	Dicotyledonous trees
4	Dicotyledonous shrubs
5	Monocotyledonous Lianes
6	Dicotyledonous Lianes and related trailing plants
7	Fern allies; Psilopsids, Lycopods & Quillworts
8	Ferns
9	Orchids
10	Grasses (non-tussock forming)
11	Grasses (tussock forming)
12	Sedges
13	Rushes and allied plants
14	Monocotyledonous herbs other than Orchids, Grasses, Sedges, Rushes and allied plants
15	Dicotyledonous herbs - Composites
16	Dicotyledonous herbs other than Composites

APPENDIX FOUR: THOMSON & FOX SITE DATA SHEET

SURFACE (Alpha) / PLOT (#) :_____ / _____ MEASURED BY:_____

SIZE OF (BOUNDED) PLOT: 10 by 10M;

RECORDED BY:_____

Survey:Robin Mitchell PHD RESEARCH

DAY/MONTH/YEAR:_____

REGION: WESTLAND NATIONAL Pk GPS Easting):_____

CATCHMENT: COOK / SUBCATCHMENT:FOX RIVER GPS; (garmin12) Northing): _____

LOCALITY: MORAINES & FLUVIAL SURFACES OF UPPER VALLEY [1]2D/3D fix (delete one) Single/Averaged position (delete one) ± _____ m

SITE DESCRIPTION			SUBSTRATE	
ASPECT (0-360°)			Lse Bldrs (1) Grav slope (2) Alluv dep'n (3)	
SLOPE ANGLE (°) / TYPE Conv (1), Conc (2), Lin (3), Und (4)		/	Median sediment size (cm diam)	
ALTITUDE			Sediment with no sig soil cover (%)	
PHYSIOGRAPHY	Terrace (1), Moraine crest (2), Levee (3)		SOIL cover (%)	
DRAINAGE	Good (1), Moderate (2), Poor (3)		OTHER cover (e.g tree roots) (%)	
CULTURAL	None (1), Grazed (2), Tracked (3)		SOIL SAMPLES TAKEN?	YES / NO

GROUND COVER % (@ 10cm)		SOIL DEPTH (cm) av of 5 readings/cnr		BROWSE	
Vascular plants		Corner 1		Plant species	SEVERITY (1=low / 2 / 3)
Non-Vasc plants		Corner 2			
Litter		Corner 3			
Exposed Soil		Corner 4			
Exposed Rock		MID			

NOTES (including cultural)

LOCATION DIAGRAM

SPECIES COMPOSITION

COVER To nearest % ,or if <1% area covered in cm. (e.g '50 x 50'). Measure climbers/parasites within tiers.

For 10 x 10m plot: 1% = 1 by 1m; 5% = 5 by 1m/ 10 by 0.5M/ 2.5 by 2m; 10% = 2 by 5m/ 10 by 1m/ 2.5 by 4m.

	EMERGENT/ CANOPY	SUB-CANOPY	SM TREE	SHRUB			GROUND		
TOP HT									
BTM HT									
MN TOP									
MEAN BTM									
Tot cover									
SPP, COVERS...									

DATE:_____ MEASURED / RECORDED BY:_____ / _____

SURFACE / PLOT # _____ / _____

CANOPY	SUB-CANOPY		SMALL TREE		SHRUB			GROUND / EPIPHYTE		

APPENDIX FIVE: LAKE THOMSON SITE SPECIES LIST

Species name	Development Stage				
	1	2	3	4	5
Agrostis "native canina"	✓				
Anisotome haastii	✓				
Archeria traversii			✓		
Aristotelia fruticosa			✓		
Aristotelia serrata	✓				
Asplenium bulbiferum					✓
Asplenium flaccidum		✓	✓	✓	✓
Astelia nervosa	✓	✓	✓	✓	✓
Blechnum novae-zelandiae	✓	✓	✓	✓	✓
Blechnum discolor	✓	✓			✓
Blechnum fluviatile	✓	✓			
Blechnum procerum	✓	✓	✓	✓	✓
Carex solandri	✓				
Carpodetus serratus	✓	✓	✓	✓	✓
Celmisia haastii	✓				
Chionochloa conspicua	✓				
Coprosma ciliata		✓			
Coprosma colensoi	✓	✓	✓	✓	✓
Coprosma cuneata	✓	✓	✓	✓	✓
Coprosma foetidissima	✓	✓	✓	✓	✓
Coprosma lucida	✓	✓	✓	✓	✓
Coprosma pseudocuneata	✓	✓	✓	✓	
Coprosma rhamnoides		✓	✓	✓	✓
Coprosma rotundifolia	✓				
Coprosma rugosa	✓				
Coriaria arborea	✓	✓	✓		
Corybas sp.					✓
Ctenopteris heterophylla		✓	✓	✓	✓
Cyathea smithii	✓	✓	✓	✓	✓
Cyathodes juniperina	✓	✓	✓	✓	
Dendrobium cunninghamii		✓	✓	✓	✓
Deyeuxia avenoides	✓				
Dracophyllum longifolium	✓	✓	✓	✓	
Earina autumnalis		✓	✓	✓	✓
Earina mucronata		✓	✓	✓	✓
Elaeocarpus hookerianus		✓	✓	✓	✓
Eleocharis gracilis	✓				
Epilobium brunnescens	✓				
Fuchsia excortica	✓				
Gahnia procera	✓	✓	✓	✓	

Gaultheria antipoda	✓	✓	✓	✓	✓
Gaultheria rupestris	✓	✓	✓	✓	
Gentiana montana	✓	✓	✓		
Gnaphalium sp.	✓				
Grammitis billardieri		✓	✓	✓	✓
Grammitis magellanica subsp. *nothofageti*		✓	✓	✓	✓
Griselinia littoralis	✓	✓	✓	✓	✓
Gunnera monoica	✓				
Hebe salicifolia	✓				
Histiopteris incisa	✓				
Hymenophyllum demissum		✓	✓	✓	✓
Hymenophyllum dilatatum			✓	✓	✓
Hymenophyllum flabellatum		✓	✓	✓	✓
Hymenophyllum lyallii		✓		✓	✓
Hymenophyllum multifidum		✓	✓	✓	✓
Hymenophyllum rarum			✓	✓	✓
Hymenophyllum revolutum					✓
Hymenophyllum sanguinolentum		✓	✓	✓	✓
Hypolepis ambigua	✓	✓			
Isolepis cernua	✓				
Juncus gregiflorus	✓				
Juncus novae-zelandiae	✓				
Leptospermum scoparium	✓	✓	✓	✓	
Libertia ixioides					✓
Luzula crinita var. *petrieana*			✓		
Luzula picta var. *limosa*	✓				
Luzuriaga parviflora	✓	✓			
Lycopodium scariosum	✓	✓	✓	✓	
Lycopodium varium	✓	✓		✓	✓
Lycopodium volubile		✓	✓		
Melicytus lanceolatus	✓				
Metrosideros diffusa		✓		✓	
Metrosideros umbellata	✓	✓	✓	✓	✓
Myrsine divaricata	✓	✓	✓	✓	✓
Nertera ciliata	✓	✓			
Nertera depressa	✓	✓	✓	✓	
Nertera villosa	✓	✓	✓		✓
Nothofagus menziesii	✓	✓	✓	✓	✓
Nothofagus solandri var. *cliffortioides*	✓	✓	✓	✓	✓
Olearia arborescens	✓	✓	✓	✓	
Olearia ilicifolia	✓	✓			
Ourisia crosbyi	✓				
Parahebe catarractae	✓				
Parahebe sp.	✓				
Pennantia corymbosa			✓		

Phormium cookianum	✓	✓			
Phyllocladus alpinus	✓	✓	✓	✓	✓
Microsorum pustulatum				✓	✓
Pimelea gnidia		✓	✓		
Poa colensoi	✓				
Poa incrassata	✓				
Podocarpus hallii			✓	✓	✓
Podocarpus sp.	✓	✓	✓	✓	✓
Polystichum vestitum			✓		
Pratia angulata		✓	✓		
Prumnopitys ferruginea	✓				
Pseudopanax colensoi	✓	✓	✓	✓	✓
Pseudopanax crassifolius	✓	✓	✓	✓	✓
Raukaua edgerleyi		✓			
Raukaua simplex	✓	✓	✓	✓	✓
Pseudowintera colorata		✓	✓	✓	✓
Pyrrosia eleagnifolia			✓		✓
Ranunculus reflexus	✓				
Rubus cissoides	✓	✓		✓	
Rumohra adiantiformis		✓			
Rytidosperma gracile	✓				
Schefflera digitata					✓
Schizeilema reniforme	✓				
Schoenus pauciflorus	✓	✓	✓		
Senecio sp.	✓				
Thelymitra spp.	✓				
Tmesipteris tannensis		✓	✓	✓	✓
Uncinia filiformis	✓	✓	✓	✓	✓
Uncinia rupestris	✓	✓	✓	✓	✓
Weinmannia racemosa	✓	✓	✓	✓	✓
Total number of species (S_{obs})	**77**	**68**	**63**	**55**	**52**

APPENDIX SIX: GODLEY VALLEY SITE FIELD DATA RECORDING SHEET

UNIQUE PLOT NUMBER		(2+3)	**LOCATION DIAGRAM**
CATCHMENT		(< 12)	
SUBCATCHMENT		(< 12)	
DATE		(D/M/Y)	
OBSERVER/RECORDER		(2/2)	
NZMS EASTING		(6)	
NZMS NORTHING		(6)	
ALTITUDE (m)		(4)	
ASPECT		(3)	
SLOPE		(2)	
DRAINAGE		(1)	
GROUND COVER %	VASCULAR	(2)	
	MOSS	(2)	
	LICHEN	(2)	
	LITTER	(2)	
	BARE SOIL (DEVELOPED)	(2)	
	TOTAL SURFACE ROCK/SEDIMENT	(2)	
ROCK/SEDIMENT %	Fines <2mm	(2)	Grazing
	Gravel/Coarse gravel 2-20mm	(2)	Naturalness
	Pebbles 20-60mm	(2)	Lichens
	Cobbles 60-200mm	(2)	
	Boulders >200mm	(2)	
	Bedrock	(2)	Landform Element (EL) & Development stage (DS) notes:
SOIL/FINES DEPTH (cm)	A	(3)	
	B	(3)	
	C	(3)	
	D	(3)	
	Mid	(3)	
LANDFORM COMPONENT		(1)	
LANDFORM ELEMENT		(2)	
FLOODPLAIN DEVELOPMENT STAGE		(1)	

LANDFORMS

Component (element numbers)		**Element**				
1. Active river-bed	3. Terrace Tread (1,2)	1. Prior channel	3. Flood channel	6. Flood basin	9. Permanent stm.	
2. Floodplain (1-9)		2. Prior bar	4. Braid island	5. Ephemeral stm.	7. Wetland	8. Levee

DRAINAGE

1. Good – Water passes through the substrate readily or rapidly (hours). Does not accumulate on the surface following rain.
2. Medium – Water passes through the substrate slowly (days). May accumulate on the surface but disperses slowly following rain.
3. Poor – Water passes through the substrate slowly (wks) or not at all. Substrate wet at shallow depths or free water ponding.

FLOODPLAIN DEVELOPMENT STAGE

1. Active riverbed – Presently active river bed formed of braid bars and channels. Little or no vegetation colonising riverbed cobbles. No Lichens. Frequently reworked and stable for less than 3 years.
2. Stabilising riverbed – Fine sediments begin to fill gaps between cobbles though cobbles almost wholly exposed. Lichens, mosses, epilobium, raoulia spp colonising. Over bar flow occurs frequently during discharges well below mean annual flood. Stable for 3-30 years
3. Incipient floodplain - 50-100% vegetative cover. Depth of fine sediment shallow, <7cm. Large stones exposed on floodplain surface. Overbank flow with discharges less than mean annual flood. Large raoulia mats (to several metres), grasses, matagouri seedlings. Channels not infilled. Stable 30-50 years
4. Established floodplain – Well vegetated, bare sediment only in areas of splay deposition or scour. Fine sediment depths 10-30cm. Discernible channel bank separates this stage from active river bed. Some sites still receive overbank flow from discharges less than mean annual flood. Small matagouri, grasses more abundant than raoulia mats Sedges along margins of infilling channels. 50-150 years old
5. Mature floodplain – Vertical relief obscured by infilling of channels with sediment. Fine sediment depth 20cm – 2 m in infilled channel braids. Floods greater than mean annual flood needed for overbank flow. Dense ground cover, large matagouri up to 3M. Seedlings absent due to competition by grasses. 100-250 years old.
6. River terrace - relict floodplain - Sites no longer receive overbank flow. Separated from floodplains by risers which exceed the rivers discharge potential for overbank flow.

NOTES:

VEGETATION DESCRIPTION						
	Tier 3		Tier 2		Tier 1	
TIER HEIGHT						
TIER COVER						
SPECIES COVER	Species name	Area estimate	Species name	Area estimate	Species name	Area estimate

APPENDIX SEVEN: GODLEY VALLEY SITE SPECIES LIST

Species name	Development stage				
	1	2	3	4	5
Acaena fissistipula			✓	✓	✓
Acaena inermis				✓	✓
Acaena saccaticupula				✓	✓
Aciphylla aurea			✓	✓	✓
Aciphylla montana				✓	
Agrostis capillaris		✓	✓	✓	✓
Aira caryophyllea			✓	✓	
Anisotome aromatica				✓	
Anisotome flexuosa			✓		
Anthoxanthum odoratum		✓	✓	✓	✓
Brachyglottis bellidioides			✓	✓	✓
Brachyscome longiscapa				✓	
Cardamine debilis		✓			
Carex decurtata		✓	✓		
Carex enysii				✓	
Carmichaelia spp. *'australis'*	✓	✓	✓	✓	✓
Celmisia gracilenta				✓	
Celmisia haastii			✓	✓	
Celmisia sessiliflora			✓		
Cerastium fontanum subsp. *vulgare*	✓	✓	✓	✓	✓
Chionochloa rigida					✓
Cirsium vulgare					
Colobanthus acicularis		✓			
Colobanthus buchananii			✓		
Colobanthus strictus		✓	✓	✓	
Coprosma acerosa	✓	✓	✓	✓	✓
Coprosma atropurpurea	✓	✓	✓	✓	✓
Coprosma perpusilla			✓		
Coriaria angustissima			✓	✓	
Coriaria plumose		✓	✓	✓	
Craspedia spp.	✓	✓	✓	✓	
Crepis capillaries			✓	✓	✓
Dactylis glomerata				✓	✓
Deyeuxia avenoides					✓
Dianthus armeria				✓	✓
Discaria toumatou		✓	✓	✓	✓
Dracophyllum kirkii				✓	
Dracophyllum longifolium				✓	✓
Dracophyllum uniflorum			✓	✓	✓
Elymus solandri		✓	✓	✓	✓

Epilobium melanocaulon	✓	✓	✓		
Epilobium microphyllum	✓	✓	✓		
Epilobium rostratum	✓		✓		
Epilobium tenuipes			✓	✓	✓
Euphrasia zelandica			✓	✓	✓
Festuca matthewsii				✓	✓
Festuca novae-zelandiae		✓	✓	✓	✓
Festuca rubra subsp. *commutata*		✓	✓		✓
Festuca sp. *'native rubra'*			✓		
Galium perpusillum				✓	✓
Gaultheria crassa			✓	✓	✓
Gaultheria depressa var. *novae-zelandiae*				✓	
Gentiana grisebachii				✓	✓
Geranium sessiliflorum			✓	✓	✓
Gingidia decipiens			✓	✓	
Gnaphalium traversii				✓	
Hebe buchananii			✓		✓
Hebe lycopodioides			✓		
Hebe subalpina			✓		
Helichrysum bellidioides				✓	
Helichrysum depressum	✓	✓	✓		
Helichrysum filicaule			✓	✓	✓
Hieracium pilosella	✓	✓	✓	✓	✓
Hieracium praealtum	✓	✓	✓	✓	✓
Holcus lanatus	✓	✓	✓	✓	✓
Holcus mollis				✓	✓
Hydrocotyle novae-zelandiae var. *montana*	✓	✓	✓	✓	✓
Hypericum perforatum	✓	✓	✓	✓	✓
Hypochoeris radicata			✓	✓	✓
Juncus articulatus					✓
Juncus effuses				✓	✓
Juncus pusillus				✓	
Juncus tenuis				✓	
Lachnagrostis lyallii	✓	✓	✓	✓	✓
Leucopogon colensoi					✓
Leucopogon fraseri		✓	✓	✓	✓
Linum catharticum		✓	✓	✓	✓
Luzula banksiana var. *rhadina*			✓	✓	✓
Luzula migrate					✓
Luzula picta var. *limosa*			✓	✓	✓
Luzula rufa var. *albicomans*	✓	✓	✓	✓	✓
Luzula rufa var. *rufa*	✓	✓	✓	✓	✓
Luzula traversii			✓		
Lycopodium australianum			✓		
Lycopodium fastigiatum			✓	✓	

Microtis oligantha				✓	
Muehlenbeckia axillaris	✓	✓	✓	✓	✓
Myosotis uniflora		✓	✓		
Neopaxia australasica				✓	
Oreomyrrhis colensoi				✓	
Oreomyrrhis rigida			✓	✓	✓
Ozothamnus leptophyllus			✓		
Parahebe decora		✓	✓	✓	✓
Parahebe lyallii		✓			
Phleum pratense					✓
Phormium cookianum					✓
Pimelea oreophila				✓	
Pimelea sp. *'Canterbury'*		✓	✓	✓	✓
Plantago lanigera	✓				
Poa cita			✓	✓	✓
Poa colensoi		✓	✓	✓	✓
Poa kirkii				✓	✓
Poa lindsayi	✓	✓	✓		
Poa maniototo		✓	✓		
Prasophyllum colensoi				✓	✓
Pratia angulata				✓	✓
Ranunculus multiscapus				✓	✓
Raoulia glabra		✓	✓		
Raoulia haastii	✓	✓	✓	✓	
Raoulia hookeri	✓	✓	✓	✓	✓
Raoulia tenuicaulis		✓		✓	
Rumex acetosella		✓	✓	✓	✓
Rytidosperma buchananii	✓	✓	✓	✓	✓
Rytidosperma pumilum			✓		
Rytidosperma setifolium	✓	✓	✓	✓	✓
Schoenus pauciflorus				✓	✓
Scleranthus brockiei			✓	✓	✓
Scleranthus uniflorus				✓	✓
Stellaria gracilenta	✓	✓	✓		
Trifolium dubium				✓	✓
Trifolium repens	✓	✓	✓	✓	✓
Trisetum tenellum	✓	✓	✓		
Uncinia divaricata			✓	✓	✓
Viola cunninghamii				✓	✓
Wahlenbergia albomarginata		✓	✓	✓	✓
Total number of species (S_{obs})	**30**	**53**	**88**	**97**	**82**

APPENDIX EIGHT: FOX VALLEY SITE SPECIES LIST

Species name	Development stage					
	1	2	3	4	5	6
		✓	✓			
Agrostis capillaris	✓	✓				
Anisotome aromatica	✓					
Anthoxanthum odoratum		✓				
Aristotelia serrata		✓	✓	✓	✓	✓
Asplenium bulbiferum	✓	✓	✓	✓	✓	✓
Asplenium flaccidum		✓	✓	✓	✓	✓
Asplenium polyodon				✓	✓	✓
Astelia fragrans			✓	✓	✓	✓
Astelia solandri					✓	✓
Blechnum novae-zelandiae		✓	✓	✓		✓
Blechnum chambersii		✓	✓	✓	✓	
Blechnum colensoi				✓		
Blechnum discolor			✓		✓	✓
Blechnum fluviatile			✓	✓	✓	
Blechnum penna-marina		✓	✓			
Carex cockayneana		✓				
Cardamine debilis		✓		✓	✓	
Cardiomanes reniforme			✓	✓	✓	✓
Carmichaelia arborea		✓	✓	✓	✓	✓
Carpodetus serratus	✓	✓	✓			
Celmisia du-rietzii (?)	✓					
Celmisia sp.		✓				
Celmisia verbascifolia ssp. *verbascifolia*		✓				
Cerastium fontanum ssp. *vulgare*	✓	✓				
Chionochloa conspicua	✓	✓	✓			
Cirsium vulgare	✓	✓				
Clematis paniculata		✓	✓			
Coprosma ciliata			✓			
Coprosma colensoi					✓	✓
Coprosma cuneata			✓	✓		
Coprosma foetidissima			✓	✓	✓	✓
Coprosma lucida		✓	✓	✓	✓	✓
Coprosma propinqua		✓	✓			
Coprosma rotundifolia			✓	✓	✓	✓
Coprosma rugosa	✓	✓	✓			
Coriaria arborea	✓	✓	✓	✓		
Corybas orbiculatus			✓	✓		
Coriaria plumosa		✓				

Cortaderia richardii	✓	✓				
Corybas trilobus			✓	✓		
Leptinella squalida ssp. *mediana*		✓				
Crepis capillaris		✓				
Ctenopteris heterophylla			✓	✓	✓	✓
Cyathea medullaris				✓	✓	
Cyathea smithii			✓	✓	✓	✓
Dacrydium cupressinum					✓	✓
Dacrycarpus dacrydioides						✓
Dendrobium cunninghamii			✓		✓	✓
Dicksonia squarrosa			✓	✓	✓	✓
Earina autumnalis			✓	✓	✓	✓
Earina mucronata			✓	✓	✓	✓
Epilobium alsinoides ssp. *atriplicifolium*		✓				
Epilobium brunnescens	✓	✓				
Epilobium glabellum	✓	✓				
Epilobium microphyllum	✓	✓				
Epilobium pedunculare		✓				
Epilobium sp.	✓					
Festuca matthewsii		✓				
Fuchsia excorticata		✓				
Gaultheria rupestris	✓	✓	✓			
Geum cockaynei		✓				
Gingidia montana		✓				
Gnaphalium audax		✓				
Gnaphalium hookeri		✓				
Gnaphalium limosum		✓				
Gnaphalium luteo-album	✓	✓				
Gnaphalium trinerve			✓			
Grammitis billardierei			✓	✓	✓	✓
Grammitis magellanica			✓		✓	
Griselinia littoralis		✓	✓	✓	✓	✓
Gunnera dentata		✓				
Gunnera monoica		✓				
Hebe salicifolia	✓	✓	✓	✓		
Hebe subalpina		✓				
Hedycarya arborea		✓	✓	✓	✓	✓
Helichrysum bellidioides	✓	✓				
Hieracium pilosella		✓				
Hieracium praealtum	✓	✓				
Histiopteris incisa			✓		✓	✓
Hoheria glabrata			✓	✓	✓	
Holcus lanatus	✓	✓				
Hydrocotyle moschata			✓			
Hydrocotyle novae-zelandiae var. *montana*		✓				

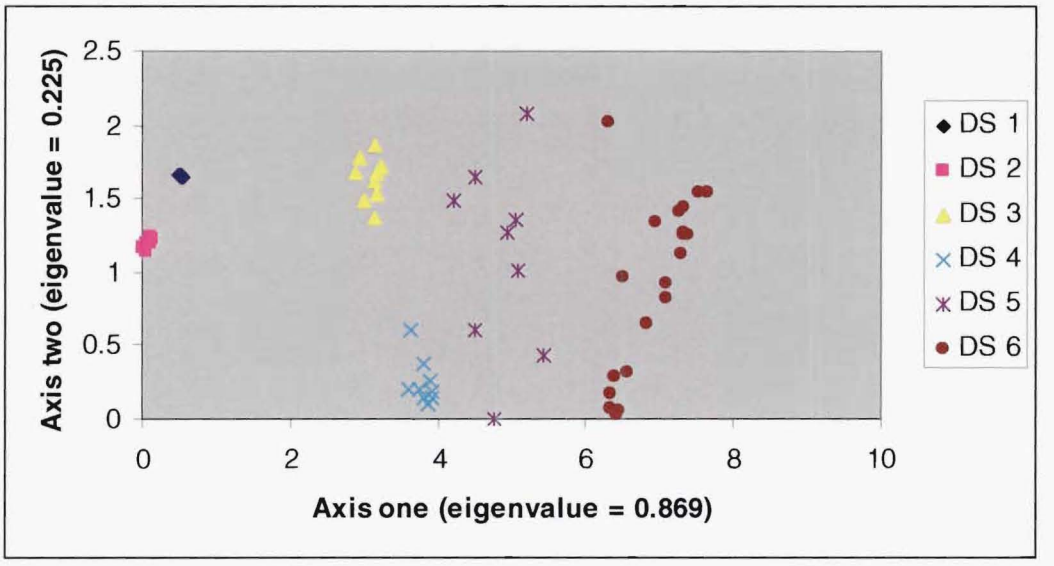
Hymenophyllum demissum			✓		✓	✓
Hymenophyllum dilatatum				✓	✓	✓
Hymenophyllum ferrugineum				✓	✓	✓
Hymenophyllum flabellatum				✓	✓	✓
Hymenophyllum flexuosum				✓	✓	
Hymenophyllum lyallii				✓	✓	✓
Hymenophyllum multifidum			✓	✓	✓	✓
Hymenophyllum pulcherrimum				✓		
Hymenophyllum revolutum			✓		✓	✓
Hymenophyllum sanguinolentum			✓	✓	✓	✓
Hymenophyllum scabrum			✓	✓	✓	✓
Hypolepis millefolium			✓			
Hypochoeris radicata	✓	✓				
Hypolepis rufobarbata					✓	✓
Lachnagrostis lyallii	✓	✓				
Lagenifera petiolata	✓	✓	✓			
Lastreopsis hispida				✓	✓	✓
Leontodon taraxacoides		✓				
Leptopteris hymenophylloides						✓
Leptolepia novae-zelandiae				✓	✓	
Leptopteris superba					✓	✓
Lindsaea trichomanoides						✓
Luzula banksiana var. *migrate*	✓					
Luzuriaga parviflora					✓	✓
Luzula picta var. *picta*		✓				
Lycopodium varium			✓	✓	✓	
Melicytus ramiflorus		✓	✓	✓	✓	✓
Metrosideros diffusa					✓	✓
Metrosideros fulgens				✓		✓
Metrosideros perforata					✓	✓
Metrosideros umbellate		✓	✓	✓	✓	✓
Microlaena avenacea			✓	✓		✓
Microtis unifolia	✓	✓				
Muehlenbeckia australis		✓				✓
Muehlenbeckia axillaris	✓					
Myrsine australis			✓		✓	✓
Myrsine divaricata		✓	✓	✓	✓	✓
Pseudopanax colensoi		✓	✓	✓	✓	✓
Neomyrtus pedunculata						✓
Nertera ciliata		✓	✓		✓	
Nertera depressa		✓	✓	✓	✓	
Nertera villosa		✓	✓	✓	✓	✓
Olearia arborescens	✓	✓	✓			
Olearia avicenniifolia	✓	✓	✓	✓		
Olearia ilicifolia	✓	✓	✓			

Olearia moschata	✓					
Parahebe linifolia	✓	✓				
Parahebe lyallii	✓	✓				
Pennantia corymbosa		✓	✓	✓	✓	
Microsorum pustulatum		✓	✓	✓	✓	✓
Pittosporum colensoi		✓	✓			
Pneumatopteris pennigera				✓		
Poa cockayneana	✓					
Poa novae-zelandiae	✓					
Podocarpus totara var. *waihoensis*			✓			
Polystichum vestitum	✓	✓	✓	✓	✓	
Pratia angulata		✓		✓		
Prumnopitys ferruginea					✓	✓
Prunella vulgaris			✓			
Pseudowintera axillaris						✓
Pseudowintera colorata				✓	✓	✓
Pseudopanax crassifolius					✓	✓
Raukaua edgerleyi						✓
Raukaua simplex			✓		✓	✓
Pterostylis spp.			✓	✓		
Pyrrosia eleagnifolia			✓			✓
Ranunculus reflexus		✓	✓			
Raoulia hookeri	✓	✓				
Raoulia tenuicaulis	✓	✓				
Ripogonum scandens				✓	✓	✓
Rubus cissoides				✓	✓	✓
Rumohra adiantiformis			✓	✓	✓	✓
Rytidosperma gracile	✓	✓				
Rytidosperma setifolium	✓	✓				
Schefflera digitata		✓	✓	✓	✓	✓
Schoenus pauciflorus		✓				
Scirpus sp.		✓				
Senecio minimus		✓				
Senecio wairauensis		✓	✓			
Sonchus asper		✓				
Sonchus oleraceus		✓				
Thelymitra spp.			✓			
Tmesipteris tannensis					✓	✓
Trichomanes strictum						✓
Trichomanes venosum			✓	✓	✓	✓
Uncinia divaricata	✓	✓				
Uncinia uncinata		✓	✓	✓		
Weinmannia racemosa		✓	✓	✓	✓	✓
Number of species (S_{obs})	**41**	**91**	**78**	**65**	**70**	**69**

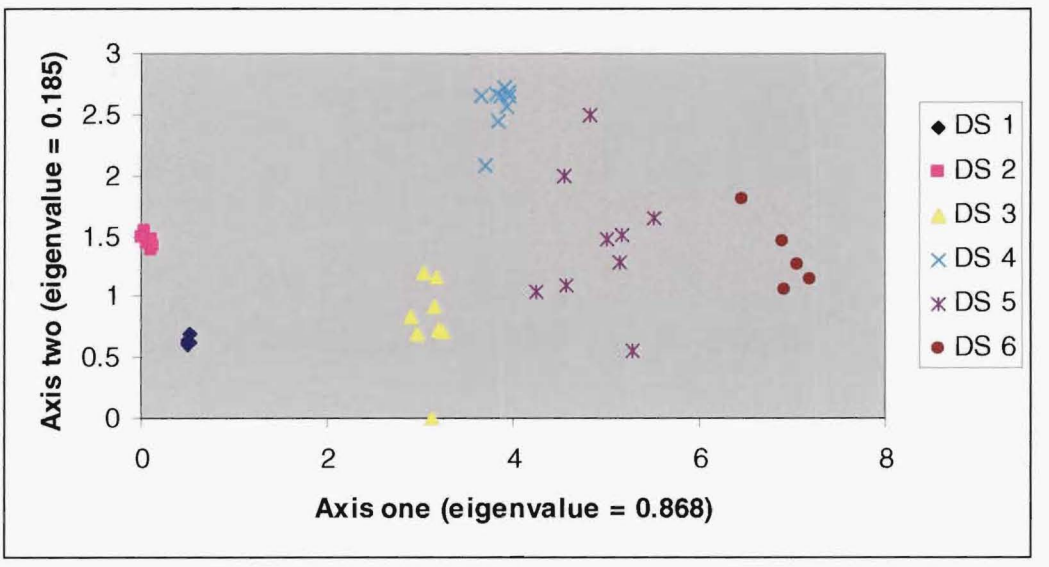
APPENDIX NINE: TEST OF PLOT SIZE SUITABILITY FOR SAMPLING FOX VALLEY SITE DEVELOPMENT STAGE SIX

Whilst it was predicted that the 10 x 10 m plot size would be sufficient to sample species diversity effectively for DS 6, a further issue was identified. It was postulated that the high proportion of the total space and biomass within a 10 x 10 m plot occupied by individuals of the largest species may result in sample data inaccurately representing the assemblage in two ways: an artificially skewed species relative abundance distribution and also a falsely high floristic variation between replicate samples. These issues are the consequence of using a uniform plot size to sample a successional gradient. Even plot size is a necessary constraint if comparisons are to be made among development stages along such a gradient.

Time was too limited to allow sampling solely for the purposes of checking the suitability of the 10 x 10 m plot size for DS 6. Therefore, a different sampling design to the other stages was adopted so that a post-hoc decision to increase plot size could be made if necessary. The design involved sampling five randomly located 20 x 20 m plots (n=5), each with four nested but individually sampled 10 x 10 m sub-plots (n=20). Comparison of the two graphs of DCA axis one and two sample scores for non-aggregated sub-plots (10 x 10 m) (Figure 1a) and aggregated plots (20 x 20 m) (Figure 1b) shows an acceptable level of floristic variation within the n=20 sample group compared to the n=5 sample group. The inter-sample floristic variation of the smaller plots is also reasonable when compared to that of DS 5, whose largest individuals comprise a lower proportion of the total plot cover than the largest individuals in DS 6. Therefore, it was concluded that the 10 x 10 m plot size was sufficient to sample DS 6. Thereafter, for all further analysis purposes, nine 10 x 10 m samples were chosen to keep the number of replicates consistent with the other development stages. The nine were chosen at random to be two diagonally opposed sub-plots from each nested plot with one subtracted. Whilst it can be argued that the selected sub-plots are not completely independent of one another, at least they do not share any boundary space.



a)



b)

Figure 1 Graphs of DCA axis 1 & 2 results showing development stage six data as either twenty 10 x 10 m plots, in Graph 'a', or as five 20 x 20 m plots where the data for the nested 10 x 10 metre plots are amalgamated, in graph 'b'.

APPENDIX TEN: ANOVA RESULTS FOR COMPARISONS OF INDICES' TRAJECTORIES AMONG ALL SITES

This appendix contains the full ANOVA (accumulated analysis of variance) results tables for the regression procedure designed to identify indices which had mathematically similar patterns between all sites. Summarised results are presented in Table 6.2. in the main thesis body. Methods are detailed in section 6.3.3.1. The format of the results is identical for each index similarity test; an explanation follows. The five rows of results immediately underneath the header row detail the change associated with adding successive terms into the regression model. The order and identity of these terms are as described in the methods section 6.3.3.1. The residual row equates to the variance in the data set left unexplained by all five regression terms. The total row is the total variance in the data set.

Importance score

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	2179.0133	1089.5067	4349.63	<.001
+ LogAge	1	538.0058	538.0058	2147.88	<.001
+ LogAge.Site	2	225.6957	112.8479	450.52	<.001
+ LogAge2	1	21.0519	21.0519	84.05	<.001
+ LogAge2.Site	2	18.5422	9.2711	37.01	<.001
Residual	244	61.1177	0.2505		
Total	252	3043.4266	12.0771		

Species density

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	16261.39	8130.70	224.91	<.001
+ LogAge	1	4204.32	4204.32	116.30	<.001
+ LogAge.Site	2	6157.12	3078.56	85.16	<.001
+ LogAge2	1	1847.80	1847.80	51.11	<.001
+ LogAge2.Site	2	375.12	187.56	5.19	0.006
Residual	236	8531.44	36.15		
Total	244	37377.20	153.19		

Simpson's Dominance

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	3.4461	1.7231	12.41	<.001
+ LogAge	1	22.8539	22.8539	164.54	<.001
+ LogAge.Site	2	12.7030	6.3515	45.73	<.001
+ LogAge2	1	8.5964	8.5964	61.89	<.001
+ LogAge2.Site	2	1.0323	0.5161	3.72	0.026
Residual	236	32.7799	0.1389		
Total	244	81.4117	0.3337		

Simpson's evenness

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	1.494127	0.747063	103.81	<.001
+ LogAge	1	0.122100	0.122100	16.97	<.001
+ LogAge.Site	2	0.241600	0.120800	16.79	<.001
+ LogAge2	1	0.002136	0.002136	0.30	0.586
+ LogAge2.Site	2	0.085780	0.042890	5.96	0.003
Residual	236	1.698330	0.007196		
Total	244	3.644072	0.014935		

Distance from the lognormal species relative abundance distribution

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	0.0376	0.0188	0.12	0.884
+ LogAge	1	5.3772	5.3772	35.22	<.001
+ LogAge.Site	2	9.1324	4.5662	29.90	<.001
+ LogAge2	1	2.8457	2.8457	18.64	<.001
+ LogAge2.Site	2	2.2590	2.1295	14.35	0.008
Residual	236	34.0351	0.1527		
Total	244	53.6870	0.2200		

Shannon's growth form diversity

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	11.02290	5.51145	88.59	<.001
+ LogAge	1	3.65595	3.65595	58.77	<.001
+ LogAge.Site	2	15.93063	7.96532	128.04	<.001
+ LogAge2	1	0.94741	0.94741	15.23	<.001
+ LogAge2.Site	2	3.14218	1.57109	25.25	<.001
Residual	236	14.68185	0.06221		
Total	244	49.38094	0.20238		

Functional richness

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	60414.2	30207.1	230.32	<.001
+ LogAge	1	6324.5	6324.5	48.22	<.001
+ LogAge.Site	2	38756.0	19378.0	147.75	<.001
+ LogAge2	1	209.2	209.2	1.60	0.208
+ LogAge2.Site	2	4446.9	2223.5	16.95	<.001
Residual	236	30951.4	131.2		
Total	244	141102.2	578.3		

Functional evenness

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	0.68455	0.34227	29.85	<.001
+ LogAge	1	0.72874	0.72874	63.55	<.001
+ LogAge.Site	2	0.45593	0.22796	19.88	<.001
+ LogAge2	1	0.00511	0.00511	0.45	0.505
+ LogAge2.Site	2	0.06216	0.03108	2.71	0.069
Residual	236	2.70609	0.01147		
Total	244	4.64257	0.01903		

Functional difference

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	144.612	72.306	37.60	<.001
+ LogAge	1	0.261	0.261	0.14	0.713
+ LogAge.Site	2	181.243	90.621	47.13	<.001
+ LogAge2	1	167.200	167.200	86.95	<.001
+ LogAge2.Site	2	87.040	43.520	22.63	<.001
Residual	236	453.797	1.923		
Total	244	1034.152	4.238		

Taxonomic distinctness

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	3046.17	1523.08	40.31	<.001
+ LogAge	1	1925.49	1925.49	50.96	<.001
+ LogAge.Site	2	4235.10	2117.55	56.04	<.001
+ LogAge2	1	185.95	185.95	4.92	0.027
+ LogAge2.Site	2	440.46	220.23	5.83	0.003
Residual	236	8917.39	37.79		
Total	244	18750.57	76.85		

DCA axis one

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ Site	2	40.0351	20.0176	65.63	<.001
+ LogAge	1	694.7710	694.7710	2277.96	<.001
+ LogAge.Site	2	21.2581	10.6291	34.85	<.001
+ LogAge2	1	0.5604	0.5604	1.84	0.177
+ LogAge2.Site	2	4.8398	2.4199	7.93	<.001
Residual	236	71.9794	0.3050		
Total	244	833.4439	3.4158		